FAO Fisheries Synopsis No. 80, Revision 1

FIRI/S80(Rev. 1)
SAST - Anguilla anguilla - 1,43(02),002,01

SYNOPSIS OF BIOLOGICAL DATA ON THE EEL
Anguilla anguilla (Linnaeus, 1758)

Prepared by
C.L. Deelder

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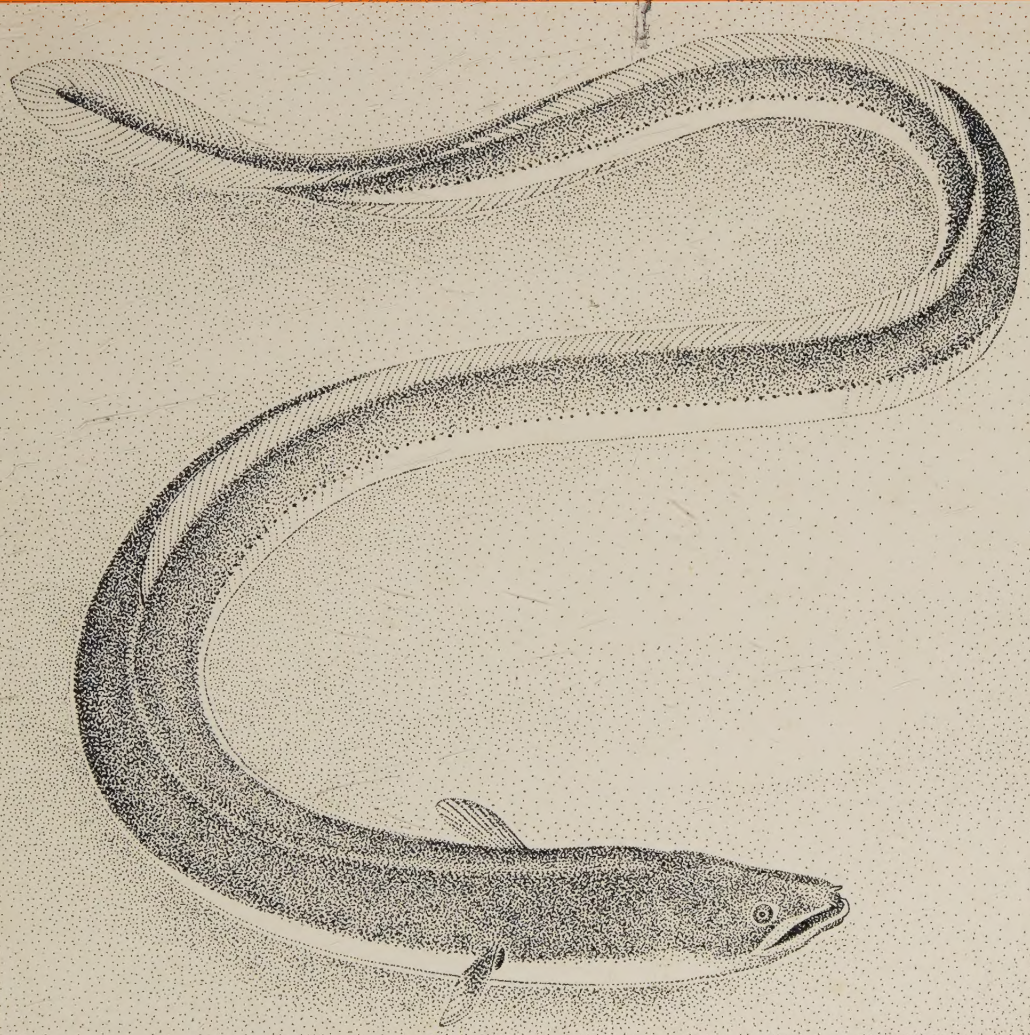

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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Anguilla anguilla (Linnaeus, 1758)

prepared by

C.L. Deelder
Netherlands Institute for Fishery Development
Haringkade 1
NL 1970 AB Ijmuiden
The Netherlands

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M-40
ISBN 92-5-102166-X

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PREPARATION OF THIS SYNOPSIS

The first edition of this document, published in 1970, was prepared at the request of the European Inland Fisheries Advisory Commission. It proved to be one of the most popular FAO species synopsis and has been out of print since many years. As the author has been able to gather substantial new information on the species in the course of the last few years, it was decided this year to produce a revised version rather than a simple rerun of the original document. In order to avoid further delays in its publication, it appeared practical to simply insert the new information provided by the author in the original text, rather than retype the entire document, even if this procedure involved some shortcomings in the presentation of the publication.

ABSTRACT

This synopsis compiles and reviews the scattered information on the identity, distribution, life history, populations, exploitation, management and culture of the eel, Anguilla anguilla (Linnaeus, 1758), a species that has been harvested in Europe for many centuries.

Distribution:

FAO Fisheries Department
FAO Regional Fisheries Officers
Regional Fisheries Councils
and Commissions
Selector SM and SI
Author

For bibliographic purposes this document should be cited as follows:

Deelder, C.L., 1984 Synopsis of biological data on the eel, Anguilla anguilla (Linnaeus, 1758). FAO Fish.Synop., (80)Rev.1: 73 p.

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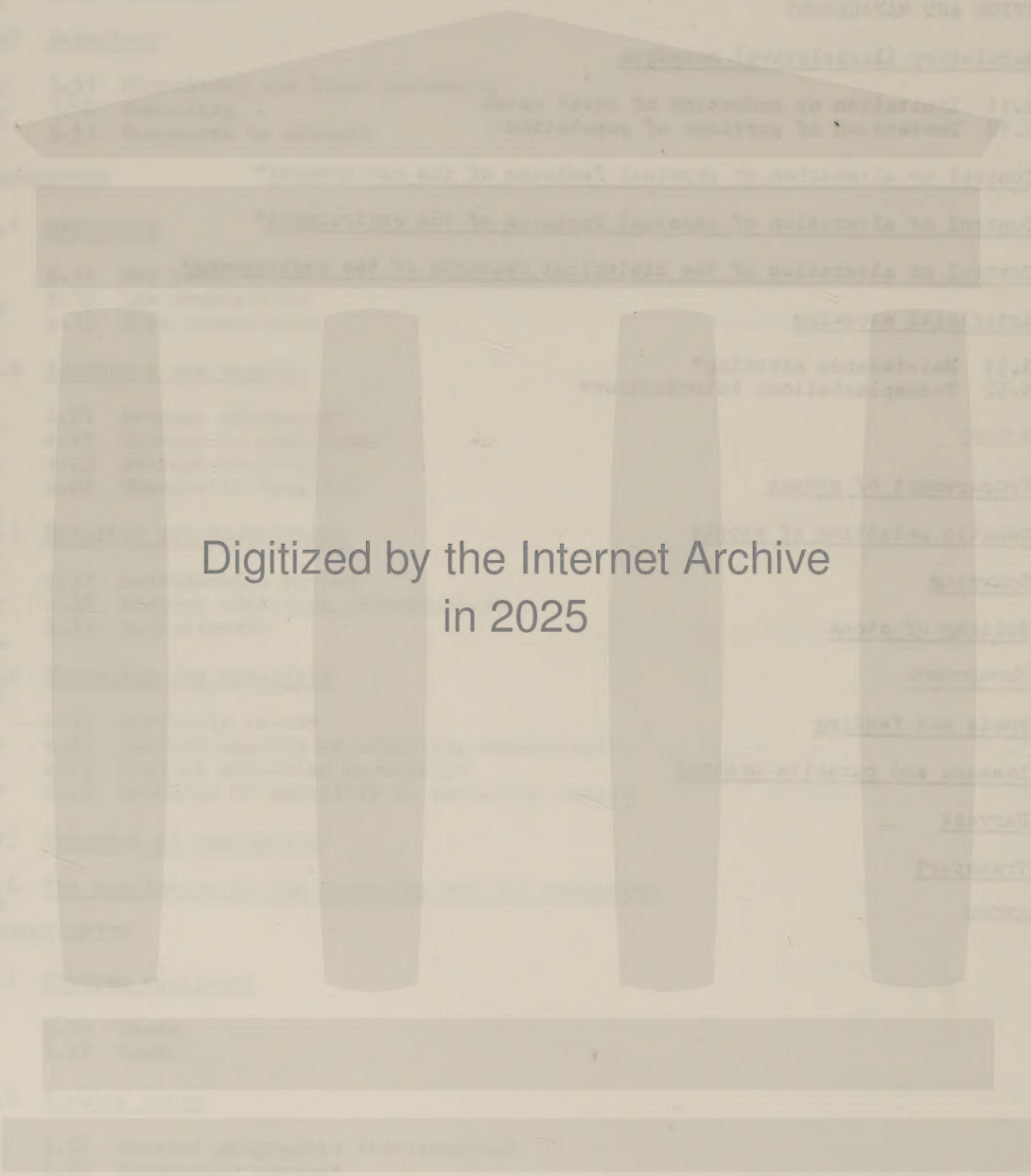
* As no information was available to the author, these items have been omitted from the text.



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1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Anguilla anguilla (Linnaeus, 1758)
(= Muraena anguilla Linnaeus, 1758, Syst. Nat. (Ed. 10): 245).

1.12 Objective synonymy

There are no junior objective synonyms of the name.

1.2 Taxonomy

1.21 Affinities

- Suprageneric

Phylum Vertebrata
Subphylum Craniata
Superclass Gnathostomata
Series Pisces
Class Teleostomi
Subclass Actinopterygii
Order Anguilliformes
Suborder Anguilloidei
Family Anguillidae

- Generic

Genus Anguilla Shaw, 1803, Gen. Zool. (Pisces), 4(1):15. Type species by monotypy: Anguilla vulgaris Shaw, 1803 (a subjective synonym of Muraena anguilla Linnaeus, 1758). Gender: feminine.

"Head smooth. Nostrils tubular. Eyes covered by the common skin. Gill-membrane ten-rayed. Body roundish, smooth, mucous. Dorsal, caudal, and anal fins united. Spiracles behind the head or pectoral fins." (Shaw, 1803).

As the family Anguillidae consists of only one genus, the family characters may be considered as generic characters too. The following (family-) concept is expressed by Berg (1949):

Body elongate, snake-like. Dorsal and anal fins confluent with the rudimentary caudal fin. Pectoral fins present, ventrals absent. Body covered with minute scales. Lateral line well-developed. Vent remote from the head. Mouth terminal; jaws not particularly elongate. Teeth small, pectinate or setiform, in several series on the jaws and the vomer. Minute teeth on the pharyngeal bones, forming an ovate patch on the upper pharyngeals. Gill openings lateral vertical, quite well developed, well separated from each other. Inner gill slits wide. Tongue present. Lips thick. Frontal bones paired, not grown together. Palatopterygoids well-developed. Premaxillaries not developed as distinct elements in adults. Pectoral girdle with 7 to 9 (up to 11 in the young) radial elements. Caudal vertebrae without transverse processes.

- Specific

Anguilla anguilla (Linnaeus, 1758). (Fig. 1)

Swainson (1839) was the first to use the combination Anguilla anguilla.

Linnaeus did not designate any type material, but a specimen named by him is in the British Museum (Natural History), London: Linnaeus Collection, No. 80.

Type locality: Europe. Linnaeus (1758) (see below) referred to the abundance of the species in Lake Comacchio, near Ferrara, Italy, but this cannot be regarded as restricting the type locality.

Definition of Muraena anguilla by Linnaeus (1758):

Anguilla. M. maxilla inferiore longiore, corpore unicolore.
D. 1000. P. 19. V. 0. A. 100. C. -.
Art. spec. 66, gen. 24, syn. 39. Fn. Svec. 290.
Muraena unicolor, maxilla inferiore longiore.
Habitat in Europa; maxima in lacu Comacchio Ferrariensi; non fert Danubium.
Nocturna; latet in coeno duplici foramine; coërcetur trunco albo Betulae; cutis tenacissima; parit vivipara, sub canicula.

Body nearly cylindrical, slightly compressed, especially near caudal end. Tail end rounded, Length 40 cm to 1 m or more. Head compressed. Snout rather elongated, sometimes broad, depressed. Jaws and vomer provided with a series of teeth. Mouth-slit extending to about level of middle of eye. Front nostril tubular near tip of snout; hind-nostril opening in front of the upper half of eye.
Eye round with yellowish iris, diameter 1/8 to 1/12 length of head; about half pre-orbital distance. External branchial aperture about as long as eye-diameter.
Pectoral with 14 to 18 fin-rays. Anterior end of dorsal fin well behind head, in front of anal opening, at about 2/5 total length. Dorsal and anal fins becoming higher near tail, where they form one rounded fin. Lateral line quite distinct. Small elliptical scales embedded in skin. Colour variable; dorsal side varying from greyish-brown, olive-brown or yellowish, to black; ventral side yellowish. Fins yellowish, dorsal fin darker.
The specimens approaching sexual maturity ('Anguilla Kieneri' Kaup, 'A. Bibroni' Kaup,

Fig. 1. Eel, after C. Gesner (1575). (By courtesy of Dr. S.J. de Groot).

etc.) have their eyes enormously enlarged (diameter much greater than pre-orbital distance), dorsal side black, ventral side white with silvery reflections (silver eels), pectorals dull, dark, even black.
Vertebral number: 112 to 117, of which 45 to 46 are pre-anal. Leptocephalus larva (Leptocephalus brevirostris Kaup), attaining 88 mm, shaped like an olive leaf. Beginning of dorsal fin always in front of anus; pectorals well developed; caudal fin deep; last hypural large, with 5 rays; last but one slit, with 4 rays; last but three with 1 ray.

(translated from d'Ancona, 1938)

Diagnosis: Vert. 111 to 119, normally 114 to 116; D 245 to 275; A 176 to 249; C 7 to 12; P 15 to 21. (Berg et al., 1949).

Prehaem. vert. 44 to 47; vert. 110 to 119; R.br. 9 to 13; P. 15 to 21. (Ege, 1939).

Vert. 112 to 117; D 245 to 275; A 205 to 235. (Wheeler, 1969).

- Subjective synonyms

Muraena anguilla Linnaeus, 1758; Anguilla vulgaris Shaw, 1803; placed in synonymy of Anguilla acutirostris Risso, 1826, by Yarrell (1836). Reasons not discussed.

Anguilla cloacina Bonaparte, 1846; Anguilla platyrhynchus Costa[1]; placed in synonymy of Anguilla latirostris Risso, 1826, by Yarrell (1849). Reasons not discussed.

Muraena oxyrhina Ekström, 1835; Anguilla acutirostris Risso, 1826; placed in synonymy of Anguilla migratoria Krøyer, 1846-1849, by Krøyer (1846-49). Reasons discussed.

Anguilla latirostris Risso, 1826; Anguilla obtusirostris Risso[1]; placed in synonymy of Anguilla fluviatilis Anslijn, 1828, by Heckel and Kner (1858). Reasons not discussed.

[1] Date of publication not known.

Anguilla fluviatilis Anslijn, 1828; Anguilla mediorostris Risso, 1826; Anguilla migratoria Krŏyer, 1846-1849; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Von Siebold (1863). Reasons not discussed.

Muraena platyrhina Ekström, 1835; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Van Bemmelen (1866). Reasons discussed.

Anguilla canariensis Valenciennes, 1836-44; Anguilla Callensis Guichenot, 1850; Anguilla Cuvieri Kaup, 1856; Anguilla Bibronii Kaup, 1856; Anguilla Savignyi Kaup, 1856; Anguilla morena Kaup, 1856; Anguilla marginata Kaup, 1856; Anguilla microptera Kaup, 1856; Anguilla altirostris Kaup, 1856; Anguilla platycephala Kaup, 1856; Anguilla nilotica Kaup, 1856; Anguilla aegyptiaca Kaup, 1856; Anguilla hibernica Couch, 1865; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Günther (1870). Reasons not discussed.

Anguilla anguilla Swainson, 1839; Anguilla Linnéi Malm, 1877; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Day (1884). Reasons not discussed.

Anguilla oxycephala de la Pylaie, 1834; placed in synonymy of Anguilla vulgaris Shaw, by Moreau (1881). Reasons not discussed.

Anguilla Kieneri Kaup, 1856; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Fries, Ekström and Sundevall (1895). Reasons not discussed.

Leptocephalus brevirostris Kaup, 1856; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Grassi and Calandruccio (1897). Reasons discussed.

Anguilla septembrina Bonaparte, 1846; Anguilla oblongirostris Blanchard, 1880; Anguilla eurystoma Heckel and Kner, 1858; placed in synonymy of Anguilla vulgaris Shaw, 1803, by Schmidt (1914). Reasons discussed.

Anguilla rostrata (Le Sueur); placed in synonymy of Anguilla anguilla (Linnaeus, 1758) by Tucker (1959). Reasons discussed. Not accepted as a synonym by present author (cf.1.31).

For a comprehensive list of synonym-authors, see: Hureau and Monod (1973).

Key to the species of Anguilla Shaw, 1803. (after Ege, 1939).

I. The average breadth of the intermaxillary-vomerine band of teeth, measured in the middle, amounts to little more than half the greatest breadth of the maxillary bands.

A. Number of prehaemal vertebrae 38 to 42, total number of vertebrae 101 to 107. Average maximum value of the preanal length without head, in percent of total length, ca. 27.0 to ca. 27.2.

* Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length ca. 9.0 .....
1. A. celebesensis KAUP.

** Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length ca. 13.0 .....
2. A. interioris WHITLEY.

B. Number of prehaemal vertebrae 40 to 44, total number of vertebrae 108 to 116. Average maximum value of the preanal length without head, in per cent of total length, ca. 25.9 .....
3. A. megastoma KAUP.

II. The average breadth of the intermaxillary-vomerine band of teeth, measured in the middle, greater than or equal to the greatest breadth of the maxillary bands.

A. Skin with variegated markings.

* The three rows of teeth forming the main part of the maxillary bands are regular, longitudinal groove distinct without interruptions; a projection on the inner side of the bands anteriorly. Primary pigment of the elvers forming a distinct mediolateral streak on the end of the tail. (Dentition not known in A. ancestralis, only represented by elvers).

1. Number of prehaemal vertebrae 37 40 ..... 4. A. ancestralis EGE. According to Williamson (1974), this should be: A. celebensis juv.
2. Number of prehaemal vertebrae 39 to 43.

a. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 11.7 to ca. 11.9 ..... A. nebulosa McCLELLAND.

x Total number of vertebrae 106 to 112 ..... 5a. A.nebulosa nebulosa McCLELLAND.

xx Total number of vertebrae 107 to 115 ..... 5b. A.nebulosa labiata PETERS.

b. Average maximum value of distance between verticals through anus and origin of dorsal fin, in per cent of total length, ca. 16.3 ... . 6. A. marmorata QUOY & GAIMARD.

** The three rows of teeth in the maxillary bands irregular, longitudinal groove less distinct with interruptions; no projection of the inner side of the

bands. The elvers without streak of primary, mediolateral pigment on end of tail ..... 7. A. reinhardti STEINDACHNER.

B. Skin without variegated markings.

* Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 9.1 to ca. 14.6.

1. Average maximum value of length of gape, in percent of head length, ca. 32 to ca. 36.
a. Maxillary bands of teeth with longitudinal groove. Average maximum value of preanal length, without head, in percent of total length, ? ca. 27 ..... 8. A. borneensis POPTA.
b. Maxillary bands of teeth without longitudinal groove. Average maximum value of preanal length without head, in percent of total length, ca. 29.
x Total number of vertebrae 100 to 106. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 14.6 9. A. mossambica PETERS.
xx Total number of vertebrae 109 to 116. Average maximum value of distance between verticals through anus and origin dorsal fin, in percent of total length, ca. 11.1 10. A. dieffenbachi GRAY.
2. Average maximum value of length of gape, in percent of head length, ca. 25 to ca. 27.
a. Maxillary bands of teeth with longitudinal groove. Average maximum value of preanal length without head, in percent of total length, ca. 26.9 ..... 11. A. japonica TEMMINCK & SCHLEGEL.
b. Maxillary bands of teeth without longitudinal groove. Average maximum value of preanal length without head, in percent of total length, ca. 30.1 to ca. 30.2
x Total number of vertebrae 103 to 111. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 9.1 12. A. rostrata (LE SUEUR).
xx Total number of vertebrae 110 to 119. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 11.2 13. A. anguilla (LINNAEUS).

** Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 0.2 to ca. 3.6.

1. Constriction of the intermaxillary-vomerine band of teeth begins on an average before the middle of the band. Average maximum values of preanal length without head, in percent of total length, ca. 27.0 to ca. 28.2. Number of prehaemal vertebrae 40 to 45.
a. Average maximum value of length of intermaxillary-vomerine band of teeth, in percent of distance from front margin of that band to posterior end of right maxillary band, ca. 82 to ca. 86. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 02 to ca. 0.8 ..... A. bicolor McCLELLAND.
x Total number of vertebrae 103 to 111 ..... 14 a. A. bicolor pacifica SCHMIDT.
xx Total number of vertebrae 106 to 115 14 b. A. bicolor bicolor McCLELLAND.
b. Average maximum value of length of intermaxillary-vomerine band of teeth, in percent of distance from front margin of that band to posterior end of right maxillary band, ca. 71. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 3.6 ... 15. A. obscura GÜNTHER.
2. Constriction of the intermaxillary-vomerine band of teeth begins on an average far behind the middle of the band. Average maximum value of preanal length without head, in percent of total length, ca. 30.3. Number of prehaemal vertebrae 44 to 48 .... A. australis RICHARDSON.
a. Average maximum value of distance between verticals through anus and dorsal fin, in percent of total length, ca. 1.2 Average maximum value of head length (measured in females), in percent of total length ca. 14 ..... 16 a. A. australis schmidti PHILLIPS.
b. Average maximum value of distance between verticals through anus and origin of dorsal fin, in percent of total length, ca. 2.6. Average maximum value of head length (measured in females) in percent of total length, ca. 12 ..... 16 b. A. australis australis RICHARDSON.

1.22 Taxonomic status

The species is well established by biological data. (cf. Schmidt, 1922; Bertelsen, 1967).

1.23 Subspecies

No subspecies exists.

1.24 Standard common names, vernacular names

Standard common names:

Algeria	- Anguille, Selbah, Bou mekhriat
Arabia	- Bou mekhriat
Austria	- Aal
Belgium	- Aal, Paling, Anguille
Czechoslovakia	- Uhor
Denmark	- Ål
Egypt	- Hannash
Eire	- Eel, Silver eel
England	- Eel, Silver eel
Esthonia	- Illa, Angerjas
Finland	- Airokas, Ankerias
France	- Anguille
Galicia	- Wengurz
Germany	- Aal, Blankaal
Greece	- Khèlia, Chéli
Iceland	- Áll
Israel	- Zlofach, Zelofah
Italy	- Anguilla, Capitone
Latvia	- Zutis
Lebanon	- Un ahmed
Lithuania	- Ungurys
Madeira	- Eiró
Malta	- Sallura
Morocco	- Anguila, Noune
Netherlands	- Aal, Paling, Schieraal
Norway	- Ål
Portugal	- Enguia, Eiró
Romania	- Ogor, Ahele, Helios, Ilan balâc, Anghila
Russia	- Ugorj
Spain	- Anguila
Sweden	- Ål
Switzerland	- Aal, Anguille, Anguilla
Tunisia	- Hanek, Sallour, Sannour
Turkey	- Yilan balyghi
Ukraine	- Ogúr
Hungarh	- Közönségés ángolna
Yugoslavia	- Jegulja

Vernacular names:

It is impossible to mention all the names ascribed to the eel in any country within its discription area (e.g. Fischer, (1961) for German names). No list of vernacular names is given here.

1.3 Morphology

1.31 External morphology (For description of spawn, larvae, and adolescents, see 3.17; 3.22; 3.23).

In addition to the descriptions and diagnosis given under 1.2, some more morphological data are shown in Table I.

One of the most controversial subjects regarding individual variation concerns broadnosed and sharpnosed eels. As these names imply, in an eelstock some individuals may be observed with a relatively broad head and others with a narrow head. (Some meristic characteristics of these different groups are mentioned in Table II).

This phenomenon has given rise to two hypotheses:

1) the differences between broad- and sharpnosed eels are genetically determined;

2) the differences originate from different feeding.

After a thorough investigation Thurow (1958) derived the following conclusions:

An eelstock mainly consists of animals with intermediate characteristics. Narrow and broadnosed eels are variants of a continuous population which shows great flexibility, and their occurrence is determined by environmental conditions, especially the prevailing food. (cf.3.11).

No data are available which conclusively point to distinct geographical variation. Differences in certain characteristics, e.g. colour of the skin, which have been alleged to show geographical variation, invariably may be ascribed to strictly local circumstances without any geographical connection. According to the theory of Tucker (1959), European and American eels should be regarded as geographical variants of the same species, but this view cannot be accepted, since the respective chromosome patterns differ from each other (A. rostrata: 2n=38, 20M+18A; A. anguilla: 2n=38, 32M+6A). (Ohno et al., 1973). Besides, Camparini and Rodinò (1980) confirmed the presence of two species of Anguilla leptocephali in the spawning zone.

No subpopulations can be distinguished.

Description of morphological changes which occur during growth:

During the eel stage no external morphological changes occur.

When maturing, however, the changes are striking

TABLE I

Some morphological data on the eel (after Ege, 1939)

	100–199	200–299	300–399 ♂	300–399 ♀	most <450 400–499 ♂	most <450 400–499 ♀	most >450 400–499 ♀	most >450 500–599 mm ♀
a)	41.72 (15)	42.83 (29)	41.93 (54)	42.63 (49)	41.56 (57)	42.77 (81)	41.56 (47)	41.60 (49)
b)	28.33 (15)	29.44 (29)	29.85 (38)	29.71 (46)	29.76 (57)	29.99 (81)	30.27 (47)	30.40 (49)
c)	10.31 (15)	11.52 (29)	11.34 (103)		11.31 (139)		11.10 (47)	11.08 (49)
d)	18.02 (15)	17.93 (29)	18.31 (103)		18.45 (139)		19.17 (47)	19.32 (49)
e)	13.39 (15)	13.39 (29)	12.27 (54)	13.00 (50)	11.78 (58)	12.79 (82)	11.29 (47)	11.20 (49)
f)	25.61 (15)	26.51 (29)	25.11 (54)	25.72 (50)	23.85 (58)	26.43 (82)	26.09 (47)	25.67 (49)

a) $\frac{a}{t} \cdot 100$ Variation of preanal length, in % of total length

b) $\frac{a-h}{t} \cdot 100$ Variation of preanal length without head, in % of total length

c) $\frac{a-d}{t} \cdot 100$ Variation of distance between verticals through anus and origin of dorsal fin, in % of total length

d) $\frac{d-h}{t} \cdot 100$ Variation of predorsal length without head, in % of total length

e) $\frac{h}{t} \cdot 100$ Variation in length of head, in % of total length

f) $\frac{g}{h} \cdot 100$ Variation in length of gape, in % of total length of head

TABLE II

Some meristic characteristics concerning the heads of broadnosed and sharpnosed eels (after Thurow, 1958)

a) Skull-measures of broadnosed eels in relation to body length (in cm).

number	length	SL	OB	SH	PFB	POB	DL	ML	PMB	DH	DAH *)
4	46.7	2.60	1.05	0.54	0.50	0.21	2.05	1.29	0.29	0.09	0.39
4	49.2	2.79	1.16	0.55	0.57	0.20	2.24	1.45	0.34	0.14	0.43
3	53.6	3.24	1.41	0.70	0.62	0.20	2.63	1.66	0.33	0.14	0.52
6	60.1	3.94	1.71	0.85	0.74	0.36	3.25	2.06	0.43	0.18	0.73
5	64.9	4.15	1.74	0.86	0.75	0.33	3.36	2.15	0.48	0.19	0.74

*) SL = skull-length; OB = occipital-broadth; SH = skull-height; PFB = postfrontal-broadth; POB = postorbital-broadth; DL = dental-length; ML = maxillar-length; PMB = praemaxillar-broadth; DH = dental-height; DAH = dental-arch-height.

b) Skull-measures of sharpnosed eels in relation to body length

number	length	SL	OB	SH	PFB	POB	DL	ML	PMB	DH	DAH *)
3	46.5	2.62	1.10	0.58	0.51	0.21	2.10	1.29	0.27	0.09	0.39
3	48.3	2.76	1.16	0.64	0.58	0.21	2.09	1.38	0.27	0.09	0.39
3	50.9	2.78	1.12	0.59	0.55	0.20	2.19	1.38	0.29	0.07	0.40
3	53.8	2.83	1.19	0.62	0.55	0.20	2.18	1.40	0.27	0.08	0.39
5	57.0	3.03	1.30	0.66	0.65	0.24	2.39	1.51	0.31	0.07	0.44
4	59.7	3.29	1.44	0.69	0.61	0.23	2.59	1.62	0.35	0.09	0.45
1	64.7	3.68	1.45	0.73	0.53	0.26	2.87	1.79	0.43	0.11	0.53

c) Relation of skull-length to skull-parts

	SL	DH	PM	POB	ML	DL	OB	PFB	SH *)
Broadnosed	100	4.32	11.42	8.04	51.3	80.8	42.3	19.3	21.1
Sharpnosed	100	2.86	10.27	7.48	49.4	78.3	41.7	19.7	21.8
**)		+1.46	+1.15	+0.56	+1.8	+2.5	+0.6	-0.4	-0.7
Diff. in %		33.9	10.1	7.0	3.5	3.1	1.4	2.1	3.3

**) Difference between values of broadnosed and sharpnosed eels

(cf. 1.2 and 3.514).

the eyes enlarge significantly during this period of life. Their diameter increases 1 to 2 mm, their weight at least doubles. The olfactory organs atrophy (Pankhurst and Lythgoe, 1983); the lateral lines become more conspicuous; the dorsal side turns black, as do the pectoral fins; the ventral side, in contrast, turns white with silvery reflections. A further obvious change is that the skin becomes tougher, harder and more shining. Havinga (1943) stated that in the great mass of eels the skin weight amounts to **2.7 to 3 percent of the animal's weight. When the skin weight reaches 4.2 percent, the eel shows the first signs of becoming silvery. In fully developed silver eels the skin accounts for over 6 percent of the total weight. The belly becomes tougher too, so that it is difficult to press it together in a silver eel, in complete contrast to the weak belly of an immature** yellow eel.

Increase of dermis-thickness was confirmed by Pankhurst (1982), who also noticed increase of scale areas from 50% to 145% in sexually maturing eels.

Occasionally eels are captured with a much more sexually advanced appearance, pre-

sumably attained by eels on their spawning-route in the sea. With regard to this "partial nuptial dress", Svärdson (1949) described the presence of very enlarged eyes with a diameter of 1 cm at least, very long and pointed black pectorals, a reddish-brown colour most prominent on the belly, and a more blunted snout.

1.32 Cytomorphology

Sick et al., (1962, 1967) studied the chromosome-number of the eel and concluded that A. anguilla has 38 diploid chromosomes.

According to Chiarelli et al. (1969) A anguilla shows 18 pairs of perfectly paired and 1 pair of dissimilar chromosomes. (Cf. also 1.31).

1.33 Protein specificity

Preliminary electrophoretic studies of the eel revealed only one haemoglobin pattern (Sick et al., 1962). An extension of this study, involving 848 eels of which 302 specimens were collected in Greece and Spain, confirmed this result.

By means of electrophoresis, serum transferrins were also studied. Four variable iron-binding fractions were detected. Five phenotypes were observed, of which the frequency distribution agreed with the distribution expected on assumption of genetic control of the main transferrins by three allelic genes. (Fine et al., 1964; Drilhon et al., 1966).

It should be mentioned that a complicating factor was encountered in a comparison of Atlantic samples and samples from two areas in the Mediterranean. (Drilhon et al., 1966, 1967, 1967a). Differences in the transferrin frequencies were found both between the Atlantic and the Mediterranean specimens and between samples from the eastern and western Mediterranean. The latter in particular involved the presence of a three banded pattern in the western group. (cf. also de Ligny,1969).

Pantelouris and Payne (1968) concluded that esterase zymograms of eel sera exhibit up to eight fractions. The individual differences observed suggest genetic polymorphism and the same applies to the esterase pattern of various tissues.

Subsequently Pantelouris et al. (1970) discovered significant differences in the frequences of phenotypes in the electropherograms between samples from Germany and samples from Iceland and Scotland.

Eel blood contains a serum, which belongs, according Wunder (1967), to a group which is very poisonous for mammals. Heating to 58 - 70°C destroys the serum.

2 DISTRIBUTION

2.1 Total area

The Atlantic from the spawning area (see 3.5.1) towards Europe and Northern Africa; coastal areas of Europe and its islands from Pechora to the Black Sea; Mediterranean and its coastal areas of Middle-East and Africa; Atlantic shore of Morocco; Canary Isles; Azores; Madeira.

Boundaries in Europe are: lower part of Pechora, Volga-system, and Black Sea, with occurrence in Danube, Dniester, Bug, Dnieper and sometimes Don.

If not barred by obstacles (e.g. weirs), inland areas may be reached by eels swimming upstream in rivers and water-courses; density of eel-stock decreases with increasing distance from the coast.

Due to the easy way in which eels may be handled, transplantations over great distances are carried out, and water-areas are stocked with eels which otherwise would be absent.

Japanese eel ponds have been stocked in 1969 for the first time with elvers from France (see also 6.5).

2.2 Differential distribution

2.21 Spawn, larvae and juveniles: see 3.1.6 and 3.5.1

2.22 Adults: see 2.1

2.3 Determinants of distribution changes

Until recently it was the general conviction that Gulf stream and North Atlantic current primarily determined the distribution of the eel larvae and in this way of the species. Due to the work of Worthington (1976), in which the existence of these flow-systems is denied, it must be assumed that the larval distribution in the Atlantic is determined by other, hitherto unknown factors (cf. 3.511), with subsequent dispersion in coastal areas after the glass eel metamorphosis, assisted by possible sea-currents near and on the continental slope.

Further distribution depends on accessibility of interior water regions and on transplantations.

All water-areas, be it in the interior or along the coast, which are fit for fish and offer a sufficient food supply, may contain eels. This applies from a warm saline lagoon on the Mediterranean coast to a cool fresh trout-brook in a mountainous region, e.g., the eutrophication of the North Sea area along the Dutch coast not only gave rise to an increase of shrimp stock, but promoted an important eel stock as well. Local winter hardships are overcome by underground hibernation.

2.4 Hybridization

No hybridization is known.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

According to d'Ancona (1943), who studied the development of eel gonads from the elver stage onward, the gonads at first have a non-differentiated appearance, with some parts tending to show male characters, some female, and some intermediate. The sexual differentiation of the gonads takes place with the development of elements of the male gametogenic series and degeneration of the female or vice versa.

Differentiation of female gonads may sometimes be recognized in eels of 20 cm or even smaller. Most eels, however, remain in a condition of sexual indetermination up till lengths of 30 cm or more. During their development, a stock of eels shows a gradual series from distinct females to distinct males linked by more or less intermediate specimens.

The conditions which d'Ancona observed point to a fairly long stage of sexual indetermination, with the coexistence of prospective female cells beside potentially masculine elements; in the latter the sexual characteristics are not evident because of delayed maturation.

All observations, moreover, lead to the conclusion that in the eel the genotypic sexual determination is very labile and that it may be influenced by phenotypic factors, which act on the germ-cells through the somatic substratum of the gonad.

Sinha and Jones (1966) concluded that the "organ of Syrski", which was supposed to be the diagnostic of maleness, is ambiguous in nature, therefore it is difficult to determine the sex of eels which have these organs. Their conclusion is fully supported by Passakas and Tesch (1980), who found not less than 16 females in 42 Elbe-eels, which previously had been determined as males in their organs of Syrski (see also Wiberg, 1983).

Fidora (see d'Ancona, 1959) concluded after stocking-experiments that different conditions of crowding affect sexual determination, viz. a dense stock results in a majority of males and decreasing population density increases the percentage of females. (cf. Parsons et al., 1977). This conception tallies with other observations, e.g. a 100 per cent female stock in an understocked area like the upper reaches of long rivers, e.g. Rhine (see also Gandolfi-Hornyold, 1929, for the Loire); a great male preponderance in the dense eel population in the estuarine area of the same river (e.g. about 95 per cent in IJsselmeer); and again an increase of females in a less populated coastal sea-area next to it. Deelder (unpublished) noticed a majority of females in an enclosed polder, which is inaccesible to eels and was deliberately kept understocked with elvers by the management.

In all probability the phenomenon mentioned above gave rise to the opinion that salinity of the surrounding water-area determines the sex of eels, which is denied by Sinha and Jones (1966).

Sexual dimorphism: In the stage nearest mature (silver eel), males and females can be recognized by their length, see under 3.12

Heermans and van Willigen (1981) demonstrated that broadnosed eels turn mainly into females, which normally are characterized by a much lower fat content than males (cf. Wiehr, 1932; 3.42). This is in agreement with the observation of Thurow (1958) who mentions that broadnosed eels have a lower fat content and reach the silver eel stage later than sharpnosed eels (cf. 1.31).

3.12 Maturity

Havinga (1945) stated that female silver eels are longer than 45 cm; the smallest he noticed had lengths of 47, 48 and 51 cm. In his opinion male silver eels are smaller than 45 cm. Deelder (unpublished) observed in the IJsselmeer male silver eels as small as 25 cm.

Ehrenbaum (1929) mentioned the investigation of 5,260 eels, among which were males of 45 cm (1), 46 cm (3), 47 cm (1) and 49 cm (1). Graphs of Mercer (unpublished) show a clear division between male and female silver eels in Lough Neagh (N. Ireland) at 47 cm. The length-frequency of male silver eels increases from 31 cm to a distinct mode at 37 to 42 cm; lengths of female silver eels reach 80 cm, and the length-frequency graph shows a distinct mode at 53 to 55 cm. The largest male silver eel observed by Frost (1945) had a length of 43.0 cm, the smallest female was 44.0 cm; "such fish are most uncommon".

In this respect it should be mentioned that nowadays Italian eel farmers manage to produce male silver eels of well over 45 cm (figure 16).

From the above, the conclusion must be drawn that attaining maturity has a connection with length, and should be primarily a matter of growth-rate in the preceding period.

For size and weight of silver eels see 3.43.

3.13/3.14 Mating/Fertilization

Not observed in the wild. Boëtius and Boëtius (1980) described artificially induced mating behaviour, from which it may be assumed that mating is promiscuous and fertilization is external.

Boëtius and Boëtius (1967) studied captive silver eels. The authors found that the maximum temperature at which normal sexual development would take place was 25° to 26°C. A mathematical approach to the data on temperature and maturation period gave an indication of an optimum temperature of about 20°C. The biological zero for experimental maturation was about 10°C.

3.15 Gonads

Kokhnenko et al. (1977) and Boëtius and Boëtius (1980) described the development of gonads and eggs after treatment with gonadotrophic hormones, both in appearance as well as in chemical composition. Kokhnenko calculated mature female eels to contain 3 million eggs per 1 kg of body weight. The ovary weight increases up to 90–120 g (normal 3–16) and colour is rose-pink due to many bloodvessels.

Meske and Cellarius (1973) as well as Bieniarz and Epler (1977) dealt with the development of male gonads and described eel spermatozoa, the average concentration of which might amount to 9 million per mm^3.

3.16 Spawning

(See also 3.14/3.15.)

Hydrographical data from the supposed spawning area for eels in the Sargasso Sea indicate a spawning depth of 100–200 m in the winter months, if an optimum spawning temperature of 20°C is presupposed.

3.17 Spawn

Kokhnenko et al. (1977) and Boëtius and Boëtius (1980) observed that the pelagic eggs have a thin chorion and a diameter of about 1.2 mm. Due to their transparency the presence of one too many oil droplets in them could be established.

According to Yevseyenko (1974), by further development eel eggs will swell to diameters of 2.3–2.9 mm.

3.2 Pre-adult phase

3.21 Embryonic phase

Unknown

3.22 Larval phase

Pro-larval phase: According to Schmidt (1923) the yolk sac of larvae contains an oil globule.

Post-larval phase: The development of the eel larvae up to an average length of 75 mm (Leptocephalus brevirostris) has been described by Schmidt (1923). See 3.5.1.

It must be borne in mind in this connection, that the leptocephalus increases in length differentially, growth in length being greater postanally than pre-anally. With regard to the position of anus and dorsal fin it has been shown that neither changes its position relative to the myomeres until metamorphosis (Ford, 1931).

Grassi and Calandruccio (1897) described the metamorphosis of eel larvae into the elver stage, which was nicely illustrated afterwards with photographs by Schmidt (1912). Besides the conspicuous change from the larval olive leaf form into the eel form of the elvers with a simultaneous decrease in length and weight (Schmidt, 1923), a remarkable change in the relative position of dorsal and anal fins and of the anus takes place; the first fin rays and anus move forward in a real movement and change their position entirely with respect to the myomeres, so that fins and anus are made to lie immediately opposite the myomeres from which they are innervated, instead of remote from them as in the leptocephalus stage (Ford, 1931). It may be concluded, therefore, that the dorsal and anal fins are temporarily held in a posterior position moving forward to their true positions during metamorphosis.

Bartels (1922), who studied the anatomy of larvae and elvers, noticed remarkable changes in some organs, e.g. the lateral line and intestines. He moreover mentioned the existence in the leptocephalus of a big jelly-filled cavity, occupying the greater part of the body and with the neurochord suspended in it. This cavity disappears completely during metamorphosis. The jelly presumably keeps the animals in the upper water layers by its low specific gravity, since leptocephali do not possess swim bladders.

3.23 Adolescent phase. Elvers.

The most conspicuous features of elver development are the gradual pigmentation (starting with the "taohe cérébrale") and the reduction in length and weight (Gilson, 1908; Strubberg, 1913). Decrease in length of elvers after reaching the Danish coast may amount to 3.5 mm (from about 7 mm to 6.5 mm); decrease of weight from about 0.32 g to 0.135 g, a deficit of 0.185 g. This reduction is due to not feeding while migrating and swimming.

At Den Oever (Holland) the greatest recorded length of immigrating elvers is 92 mm; the smallest, 56 mm. The annual average length of immigrating elvers varies here from 72 to 77 mm.

Diseases and parasites are unknown for this stage.

Predators are found in the whole scale of animals big enough to devour elvers: many kinds of fishes (although elvers are known to escape through the gill-slit) including eels (Sinha and Jones, 1967a), rats (e.g., at elver-passes), and gulls (Moriarty, 1984).

Losses due to man are very important. They may result from impassible barriers in waterways, where elvers may try to pass until they die, or by catching elvers for stocking, food or manure. An early description of this was given by Redi (1684) (cf. Bertin, 1956), who possessed a remarkable insight into eel biology. According to him, on a day in 1677 more than 3,000 Tuscany pounds (1,200 kg) of elvers were caught in the Pisa stretch of the Arno within 5 h.

The total damage inflicted to an elver stock by man and animals must be tremendous.

3.3 Adult phase (Mature fish)

Although eels and silver eels are not strictly mature fish, they will be discussed here since they represent the most important phases in the life of Anguilla anguilla.

3.31 Longevity

The total life span a.o. depends on the time taken to attain the silver eel stage. Since this, as already has been pointed out, is determined partly by sex and growth-rate, which are strongly influenced by the environment, it is difficult to give a general statement.

Absolute topper is "Putte", kept for 85 years in aquaria (Svärdson, 1949). Bertin (1956) mentioned an eel which lived 37 years in captivity, and eels staying for 50 years in a Swiss lake.

3.32 Hardiness

Provided enough oxygen is available to breathe and the skin is kept wet, with an air temperature not exceeding 15°C (Krogh, 1904), hardiness of eels and silver eels is great. It is because of this characteristic that their economic value is great too, since it enables storing, handling and transporting over huge distances. Although no exact data are available it is a well-known fact that silver eels may be densely packed in live-basins for months. Mann (1960) kept starving eels for 3 and even 4 mo in aquaria filled with tapwater. Because of their physiological state in which they need no food, silver eels may be kept longer in captivity than eels: Boëtius (1967) experimented with silver eels during 9 successive months, and Boëtius and Boëtius (1967) kept a silver eel which was able to mature normally after a period of starvation of over 3 yr.

Boëtius and Boëtius (1967) showed that the thermal amplitude of survival is roughly 0 to 30°C for both yellow and silver eels. The vegetative temperature range of the yellow eel is from about 10 to 30°C. This deduction has been nicely confirmed by the experience of Japanese eel-culturists, who in 1969 imported elvers from France. First there was great satisfaction; in the summer, however, with water temperatures of over 30°C, a great mortality occurred without signs of diseases or parasites. The conclusion was that the European eel could not withstand very well these high temperatures (Korringa, personal communication).

3.33 Competitors

Rogers (1964) correctly pointed out that one may still query the suitability of the criteria upon which competition is judged. It is obvious that what does, in fact, constitute "competition" is still subject to considerable debate. To some it seems quite wrong to assume that because the same food is found in the stomachs of different species, competition must be taking place, for there may be an abundance of that food. Conversely, if an organism is found in the stomach of one species of fish and not in another, both species occurring in the same area, it cannot be said that there is no competition; it could be that one species has been markedly successful in the competition for that item of diet.

Competitors for spawning-area are unknown.

If all animals which share items of diet with eels are to be regarded as competitors for food, then most species of fish which occur with eels must be included in this category. Of these, no list will be presented because of its extensiveness, due particularly to the diverse areas in which eels may live.

Since silver eels do not take food, no food competition exists here.

With regard to competition for shelter, it may be noted that eels like to hide themselves in the bottom, in tubes, plant-masses etc. No serious competition by other species for these habitats is known.

3.34 Predators

For the youngest eel stages, all fish which are able to swallow elvers may act as predators, although eels are more protected by their way of living. Grown eels are preyed on mostly by bigger eels (Sinha and Jones, 1967) and by birds. Cormorants may take a heavy toll as they are able to dive, and herons are important in shallow areas.

Van Dobben (1952), who studied a cormorant rookery, observed that the food composition is ruled by the accessibility of the eel. The catch of eels increases with the approach of the summer, until on warm days in July the eels become the principal food. As almost all eels caught are injured at the snout and the birds exclusively catch in daytime, it must be assumed that the eels are caught when hidden in the bottom with their head protruding. No efficacious defense reactions of the eels are known.

The length of the eels caught may range from 18 to 60 cm. Van Dobben calculated that a cormorant rookery with about 2,000 nest situated near the IJsselmeer consumes in a summer about 200,000 kg of eels.

Moriarty (1984) observed predation by gulls on elvers released for stocking purposes.

With regard to fish predation Hegemann's (1958) interesting observation must be mentioned regarding pike in the Greifswalder Bodden (Rügen) consuming eel. Eels made up 4 percent of the prey of 50 pike.

No data are known about predation as a factor controlling the eel population in any area.

3.35 Parasites, diseases, injuries and abnormalities

Parasites and diseases

These are manifold. Reichenbach-Klinke (1966) mentioned, besides common parasites such as Ichthyophthirius multifiliis, no less than 30 parasitic species:

Trypanosoma granulosum
Cryptobia markewitchi
Eimeria anguillae
Myxidium giardi
Trichodina anguillae
Trichodinella epizootica
Gyrodactylus anguillae
Triaenophorus nodulosus
Bothriocephalus claviceps
Diphyllobothrium latum (larval)
Proteocephalus macrocephalus
Sphaerostoma bramae
Plagioporus angulatus
Podocotyle atomon
Contracaecum squalii (larval)
Raphidascaris acus
Spinitectus inermis
Ichthyobronema gnedini
Camallanus lacustris
C. truncatus
Neoechinorhynchus rutili
Pseudoechinorhynchus clavula
Metechinorhynchus salmonis
Acanthocephalus anguillae
A. lucii
Pomphorhynchus laevis
Corynosoma semerme (larval)
Ergasilus gibbus
Lernaea cyprinacea
Argulus foliaceus

This list may be supplemented with other observations, e.g.: Diplostomum sp. in the eyes (Frost, 1949); cysts of Glugea sp. in eel's ovaries (Willemse, 1966); Apiosoma cylindriformis in skin and gills (Ghittino, 1970); Helicostoma buddenbrocki in skin (Purdom and Howard, 1971); Spinitectus inermis in intestines (Moravec, 1977); Ligula intestinalis and Pomphorhynchus bosniacus in intestines (Hristovski and Riggio, 1977); Sphaerostoma bramae in intestines (Lacey et al., 1982); Dermocystidium anguillae in gills (Wootten and McVicar, 1982).

Under certain conditions parasites may exert a devastating effect on eel stocks. Ichthyophthirius is able to wipe out total stocks of free-living eels (Timmermann, 1939) as well as of stored eels (Deelder, unpublished). The great massacres of eel populations, however, are caused by just a few diseases: Pseudomonas punctata and Vibrio anguillarum: "red disease" for both, and the "cauliflower disease".

According to Schäperclaus, (1954) who described this illness extensively, the "red eel disease" may be caused by the two bacterial species mentioned above. Pseudomonas thrives in water with a salinity less than 0.8 per cent NaCl, Vibrio in water with a salinity of about 1.5 to 3.5 per cent NaCl. Dutch eel merchants are well aware of this peculiarity and if possible change their stocked eels from freshwater to seawater and back again in case of "red disease", to restore the condition.

In addition to stocks of stored eels, the "red disease" may inflict heavy casualties in eel populations, e.g. in the Baltic (Wolter, 1960) and Adriatic (Canestrini, cf. Wolter, 1960) as well as in interior waters, e.g. in Holland (Deelder, unpublished).

An outbreak of the so-called "cauliflower-disease" of silver eels, starting in 1944 in Denmark, was reported by Christiansen and Jensen (1950). These silver eels presumably descended from Baltic regions. Obviously assisted by eel storage and transport, the illness attacked eels as well, and spread over Europe, to the south part of Holland in the west and toward the Black Sea in the east (Raduiescu and Angelescu, 1972), in brackish, as well as in fresh water. As indicated by the name, diseased eels bear tumors, mostly on the snout but other parts of the body might be affected as well. Despite serious efforts (cf. Schäperclaus, 1953; Koops et al., 1969; Peters and Peters, 1970, 1979; Bremer and Ernst, 1972; Einszporn-Orecka, 1974) no exact cause could be established, although a (polyhedric formed) virus might be the malefactor (Koops et al., 1969). As the tumors prevent eels from burying in the mud and from foraging, a gradual deterioration in condition is the result (cf. Lühmann and Mann, 1956). In addition, deseased eels become unsalable because of their repelling appearance.

In captivity, especially with low stocking density, conditions might be favourable to produce a stress-situation for subordinate eels (Peters et al., 1980; Peters, 1982) as well as elvers (Willemse et al., 1984), resulting in, e.g., degeneration of the gastro-intestinal tract and several other degenerative changes, which are characteristic for the General Adaptation Syndrome of Selye's stress principle.

Injuries and abnormalities

As far as known, injuries with regular appearance are only those inflicted by turbines and pumps on eels and silver eels passing downstream through power and pumping stations. These injuries may vary from complete cutting to damage visible only after some time (Butschek and Hofbauer, 1956).

Abnormalities are not common. Most conspicuous is the yellow eel, reported from time to time (e.g. Thumann, 1953). Another phenomenon observed now and then is the eel with undulated spine ("plekospondylie"). No cause is known (Schräder, 1930).

As with other animals, some abnormalities may occur occasionally: e.g. stone in the body-cavity (Tesch, 1958); kidney-disease (Scheer, 1934).

3.4 Nutrition and growth

3.41 Feeding

Eels, being nocturnal animals, feed mostly during the night, when they search for food by swimming to and fro. Aquarium experiments and direct observations (e.g. Berry, 1935), however, reveal that they feed in daytime too.

Feeding takes place all over the area where eels occur and where food is available. In estuarine areas daily movements may occur to and from the foodstaples in the brackish area (see 3.51; Koendzinsj, 1958). In springtime, spawning areas of coarse fish may attract large numbers of eels, which feed upon the spawn.

Here we may draw attention to the statement of Albertus Magnus (1545, cf. von Siebold, 1863) which runs translated: "The eel allegedly crawls out of the water during the night and enters the fields, where it finds sowed lentils, peas or beans". Nilsson (1860) pointed out that such eels might go for slugs and worms. As Deelder (unpublished) and Bergmann (1970) have proved that eels may leave the water to forage, and knowing their ability to locate the nearest stretch of water (see 3.513), it must be assumed that Magnus and Nilsson were right about this peculiar feeding ground.

The eel exhibits some peculiar ways when foraging, depending on circumstances. Small objects are taken without difficulty. A large object, e.g. a dead fish, which is too big to swallow, is attacked in the following way: the eel bites into the flesh and then tears off the mouthful by rotating around its long axis of high speed.

Buried eels catch food in a peculiar way, of which Berry (1935) gives a vivid description: "They lie buried in mud or gravel with only the tip of the snout down to the eyes projecting. The spot selected, in e.g. a river, is out of the main current, either in front of, or behind a large stone or other barrier. Any unwary creature of suitable size which passes within a few inches of this hidden danger, is seized with surprising suddenness and bolted at a gulp or swallowed gradually head first. To see an eel catapult two thirds of its length from its tunnel to seize its prey is only less remarkable than to watch it suddenly draw backwards out of sight; the flattened tail is evidently used as a sort of spring, but it is difficult to understand how they accomplish this feat".

Big eels which are not buried in the substratum presumably swim round for a while after having seized prey. Long-line fishermen cope with this habit by using special long cross-lines or by fishing exclusively for big eels on hot days, when eels are lazy, using special sized baits such as ruff or small perch.

At all times eels seem more dependent on scent than on sight for getting food. An imitation worm of other bait dangled in front of them produces little if any interest, but any object which has been placed for some time in a tin of worms causes immediate excitement. (cf. von Fritsch, 1941; Mohr, 1969).

(When baiting their longlines, fishermen should take care that their hands are clean; such things as oil or kerosene on the hands cause a sharp decrease in the catch).

Besides the scent, the taste of food also seems to play a rôle in food-uptake. Wunder (1927) showed that meat drenched in quinine is immediately spat out.

Eels in the northern part of Europe abstain from feeding in wintertime. Sinha and Jones (1967a), who studied eels from Welsh rivers, stated that feeding is mainly restricted to the months of April to September. Exceptions are known, however (Frost, 1952). It must be assumed that in the warmer southern regions of their area eels abstain from feeding for a much shorter period, if any, such to the benefit of e.g., Italian pond eel farmers.

According to the experience of fishermen using bait gear, it is obvious that in mid-summer an interruption in feeding is a common phenomenon.

3.42 Food

Eels are fully catholic with regard to animal food, provided it is alive or extremely fresh. A list of species serving as food for eel has to include virtually the whole aquatic fauna (freshwater as well as marine) occurring in the eel's area (see e.g. Frost, 1946; Sinha and Jones, 1967a; Daniel, 1968; Biró, 1974). The food list might easily be augmented with animals living out of water, e.g. worms, while fresh meat is taken as well. With eels in captivity, unlike most other creatures, there is no difficulty in inducing them to feed, and they will thrive on practically any diet.

The kind of food taken is greatly influenced by size and availability (Schiemenz, 1910). Thus, big eels are more inclined to prey on fish they can swallow than small eels, and as eels are mainly bottom dwellers they prey more on the bottom fauna. Exceptions are known, and plankton may be taken when occurring in great masses (Schiemenz, 1910). Instances of fish too big to swallow being attacked and devoured gradually by eels are also known, particularly when they are caught in gill nets (Louth Neagh, Deelder unpublished; Morrison, 1929).

Their voracity is amazing. In an aquarium, an eel of 30 cm consumed an average of 12 g, or about 25 earth worms, per day. Such an eel can consume a dozen worms each about 5 cm long in as many minutes, and after only a few hours will be ready for more (Berry, 1935).

Because of the big economic implications, the food relationships of eels and salmonids always arouse great interest. It is commonly assumed that eels cease feeding each year before the earliest salmon spawn, and that they do not become active again until after the ova have hatched (Menzies, 1933; Sinha and Jones, 1967a). This does not, however, apply to char eggs (Frost, 1952). Menzies (1933) referred to an eel trap which was for some time baited with worms without any success; when, however, some roe of a dead salmon was placed in it, it caught 44 eels between 11.00 h and 17.00 h the same day.

About salmonid fry, Berry (1935) remarked that eels account for large numbers of miller's thumbs and loach, which are amongst the most serious enemies with which alevins and young salmon and trout fry have to contend, but it must be doubted whether destruction of such enemies will make up for the numbers of small parr which eels themselves consume. Most coarse fish fry rest near the surface or among weeds, whereas young parr rest on the bottom, and it is owing to this fact that eels probably consume a high proportion.

A similar problem exists in areas with stocks of freshwater crayfish, as in Sweden. The eels are known to attack the crayfish when they have shed their shell during the moult. In this way presence of eels means a certain danger for the stock of crayfish. (cf. Svärdson, (1972).

Wiehr (1932) investigated the relation between foodfats and their biological consequences. No chemical-histological differences can be detected between broadnosed and sharpnosed eels. The latter category shows the greatest deposition of fat, particularly in the liver. Sharpnosed eels contain up to 27 per cent of fat, broadnosed eels up to 12 per cent. Eel fat consists mainly of glycerids of fatty acids, while the fat of sharpnosed eels contains more oleine.

The difference in fat-percentages of sharpnosed and broadnosed eels must be ascribed to differences in feeding: viz. the first group takes the fattest food. The quality of the eel fat moreover depends on the quality of the food fat.

3.43 Growth rate

Concerning the Leptocephalus stage, van Utrecht and Holleboom (in press) showed that at the metamorphosis the eel larvae are not of the same age. With fair certainty their age can vary from 1 to 6 years. With regard to eels, all investigators agree that eels belonging to one year group (i.e., from the glasseel stage) may show very different lengths, as has been experimentally confirmed by Meske (1968). Thus in a certain area a certain length may be "occupied" by several year-groups simultaneously. "To judge an eel's age solely by its length, would be to risk an error of one to five years either way" (Bertin, 1956; p.43).

The length-frequency of an unfished year-group of eels shows a Gaussian normal distribution; the points fall on a straight line when plotted on Gaussian paper (Deelder, 1963; figure 2).

Eels of the same length vary in weight. Examples of this are given in Table III, from the results of Marcus (quoted by Ehrenbaum, 1929), who investigated 5 260 eels. As the graphic "length" - "average weight" relation is curved (cf. Deelder and de Veen, 1958), Sinha and Jones (1967), using the equation: $W \simeq aL^n$, plotted the relation on double logarithmic paper and got straight lines for eel stocks from different areas, the lines for female eels nearly coinciding with those for male and undifferentiated eels.

Bertin (1956, p.51) concluded "that the increase in the size and weight of eels is more a question of food than anything else". The results of some investigations indeed indicate that food and its composition exert a deciding influence upon the condition of eels.

There are no indications that a high density of eel stock decreases the growth, provided there is enough food. Meyer-waarden and Koops (1968) reported on a pond on the Mosel bank with a density of no less than 1.8 eels per m^2. Food was available in plenty. Notwithstanding the crowding, the mean weight increased by 76 percent in one summer from 93.3 to 164 g.

In this respect the study of Thurow (1959) must also be mentioned. He observed that the factor K in the equation: $G = \frac{K \cdot L^3}{100}$ is dependent on age, season, environment and sex of the eels.

Negative growth-rate has been studied by Mann (1960), who kept starving eels and silver eels for 3 to 4 months in basins. His eels lost up to 20 percent of their weight. The greatest loss observed was 28 percent. Small eels decrease in weight more quickly than large ones. The same holds true for the fat content. Eels, with their lower fat content, are therefore much more affected by loss of fat than are silver eels.

The following examples concern the maximum sizes which eels may attain. Day (1880 to 1884) mentioned an eel with a length of 1.12 m, a maximum girth of 25.4 cm and a weight of 3.3 kg. He also reported an eel with a weight of 4.53 kg. Nilsson (1860) mentioned eels of 2.5 to 5.5 kg from Sweden. In 1939 an eel was caught in the Aller (Germany) with a length of 1.15 m and a weight of over 5.5 kg (Anon., 1939), and Walter (1916) mentioned three catches of eels weighing 6 kg, each in Germany. Record-holder is the 7.65 kg eel caught in Dalsland (Sweden) in the first half of the 19th Century (Svärdson, 1972).

Growth of eel in natural waters have been subjected to many investigations, either: (a) on the basis of stocking results in eel-free waters; (b) by age-determination on otoliths.

(a) Stocking results: Benecke (1881) stated that elvers, when set free in East Prussia, grew in one summer to eels of 20 cm, and reached next summer lengths up to 35-52 cm. Walter (1910) studied several stocking results and concluded that eels in (temperate) German waters could reach a length of 25 cm after the first summer, 52 cm after the second and 65 cm after the third summer (cf. Deelder, 1981). Einsele (1961) released elvers in May 1958 in the eel-free Neusiedler See and caught in 1960 eels weighing 500-800 g, with maxima up to 1 kg. Next summer the average weight was minimal 1 kg, maximum amounting to 1.5 kg. In 1961, in Lake Constance, 100 kg of elvers were released, giving a catch rise of about 100 percent (compared with 1961) in 1963, 400 percent in 1965 and 550 percent in 1966 (Berg, pers. comm.). This result cannot be ascribed to increase of catch-intensity alone. Dahl (1967), who carried out stocking experiments in Danish ponds found mean lengths at the end of the first three summers of about 17.5; 28.9 and 43.9 cm, respectively.

(b) Age-determination on otoliths: This approach is executed in order to deduce the age from the zonation in the eel otoliths, according the formula:
$L_{ot} = 0.04.L_{eel} + 0.58$ (Appelbaum and Hecht, 1978).
To promote a universal otolith preparation, the "Joint ICES/EIFAC Working Group on Eel" in 1979 unanimously agreed upon the "production of a slide of 0.2 mm thickness obtained by cutting an otolith embedded in plastic along its longitudinal axis passing through its centre so as to make clearly visible the circumferential outline of the leptocephalus otolith".

It is to be deplored that many otoliths are still treated by other methods, e.g., burning, although in this way great errors are likely to be introduced (Deelder, 1981). The major problem for age determination in this way lies in the eel's characteristic to form at times in the otoliths more than one band per year (supernumerary zones), which phenomenon caused in the past extreme errors, and, it is sad to notice, is still causing them, as recognition of that phenomenon is still eluded.

From the very beginning the age-determination on otoliths has been based on the "one band = one year" formula of Ehrenbaum and Marukawa (1914), who founded their opinion on results with basin-kept eels. This caused great errors (Deelder, 1981), as Dahl (1967) proved that in eels, transplanted as elvers to an eel-free pond, two zone-indications in one year were possible. Following this, Moriarty (1976) discovered on otoliths from Hungarian eels, that up to three zones per year could be laid down. These observations indicate that errors up to 200 percent have to be reckoned with, implying that most age-determinations hitherto have lost their significance, which also counts for future determinations if the supernumerary zonation is neglected.

As the human eye is definitely unable to distinguish between the several zones in the otoliths, special methods have to be applied to obtain a correct evaluation. Two are known and were controlled with eel otoliths of known age, respectively proposed by Wiedemann Smith (1968) and Deelder (1976; 1978b; 1981). The results obtained are in agreement with those of eel stockings (see above).

Moreover, Deelder showed that growth interruption in mid-summer occurs frequently (cf. 3.41: feeding), presumably being a main cause for supernumerary zonation.

Experiments with eels kept in basins (Kuhlmann, 1975; Sadler, 1979) showed that with sufficient foodsupply growth is regulated by temperature. When relating this datum to eel growth in open waters, it is to be reminded that monthly temperature averages in absolute value deviate only to a slight extent from the normal average, implying that usually eel growth will be nearly constant from year to year.

In this respect, Deelder (unpublished) studied growth of eels in an enclosed water area on their otoliths during the respectively "normal", "warm" and "cold" summer of 1975, 1976 and 1977 (with added average deviations for the five-month summer periods, respectively: +1.4; +3.5 and -5.0°C) and according expectancy established the feature that no obvious difference with a trend of significance could be detected in the annual length-increments. In complete contrast to fishes of other species that grow by increasing the volume of small muscle fibres already present, eels grow by forming relatively large numbers of new muscle fibres (white and red ones as well), which originate from already existing fibres by a "budding" process (Willemse and Lieuwma-Noordanus, 1983; in press).

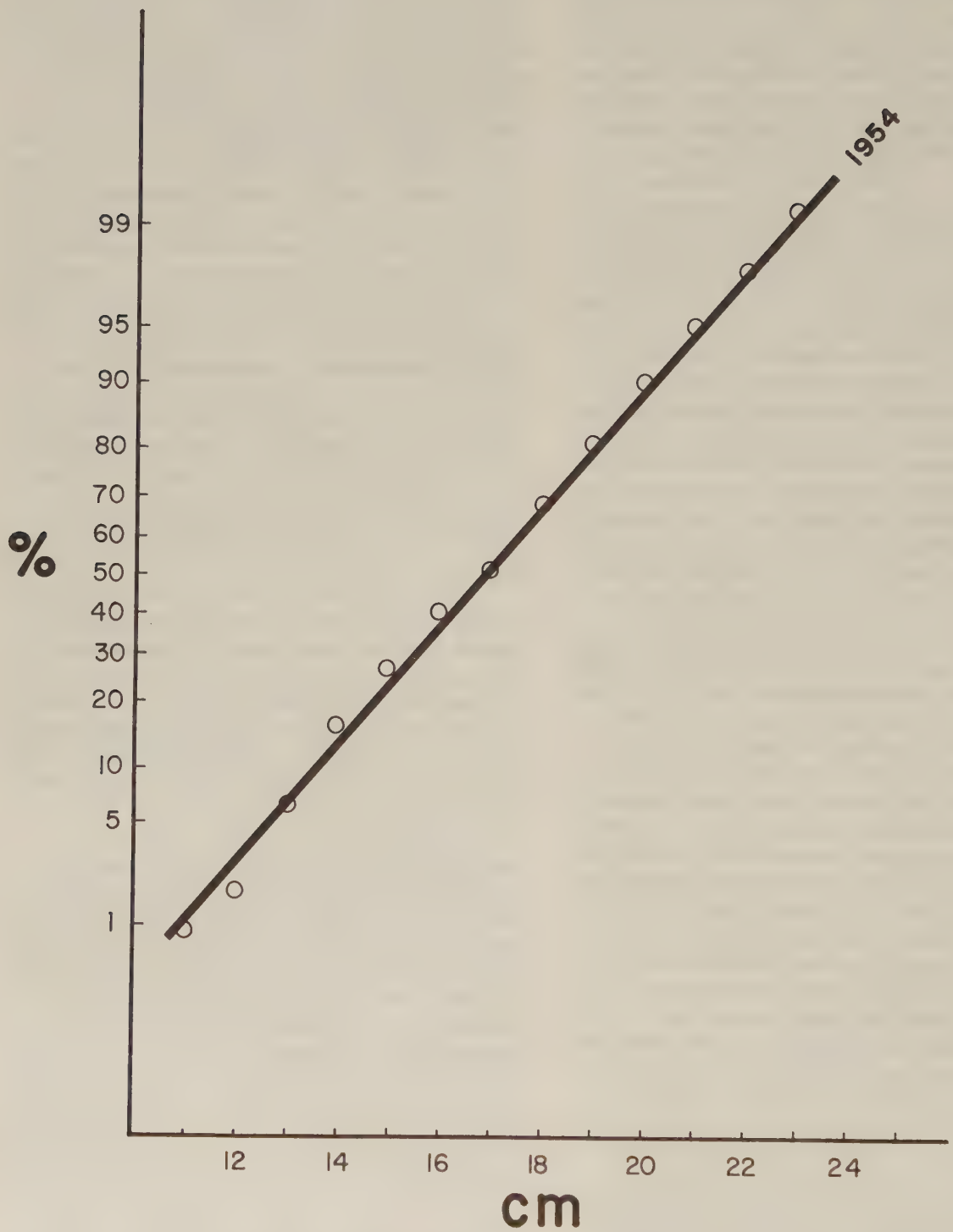

Fig. 2 Length-frequency of an unfished eel-yearclass in the IJsselmeer, plotted on Gaussian paper (Deelder, 1963).
Eel-lengths rounded off to nearest cm downwards.

TABLE III

Relation between length and weight of eels (after Marcus, in Ehrenbaum 1929)

Length (cm)	Number of investigated animals ♂	♀	Average weight (g) ♂	♀	Weight-limits (g) ♂	♀
10		10		1.2		1- 2
11		11		1.7		1- 3
12		23		2.5		1- 3
13		38		3.3		1- 5
14		44		3.8		2- 6
15		50		4.6		2- 7
16		55		5.1		3-12
17		71		6.4		3-10
18		123		7.5		4-19
19		159		8.7		4-12
20		150		12.7		6-15
21		188		12.1		7-20
22		196		13.4		5-23
23		198		15.3		9-23
24		256		17.3		11-25
25		362		20.1		12-31
26		379		22.1		14-33
27	312	92	25.5	24.4	15- 43	17- 31
28	237	113	29.2	26.8	19- 45	15- 40
29	210	141	31.8	31.1	20- 46	18- 44
30	187	139	36.0	33.2	22- 49	22- 52
31	127	139	40.0	37.5	27- 56	26- 63
32	84	108	45.5	42.9	29- 63	28- 63
33	37	86	48.2	45.6	34- 66	30- 66
34	23	86	54.5	51.5	45- 75	38- 70
35	11	92	65.5	55.6	52- 93	36- 81
36	10	74	66.0	62.1	57- 75	43- 98
37	5	53	72.4	65.3	64- 95	50-100
38	9	37	82.7	76.5	68-116	51-110
39	3	41	109.3	82.8	100-120	60-104
40	3	27	112.3	90.2	100-125	63-110
41	-	17	-	100.5	-	84-128
42	-	22	-	110.3	-	89-140
43	-	13	-	116.2	-	100-137
44	1	15	150	131.4	-	105-165
45	1	18	157	140.5	-	119-165
46	3	17	175	149.1	160-195	112-197
47	1	15	171	162.7	-	134-202
48	-	22	-	166.0	-	122-230
49	1	12	182	183.5	-	144-220
50	-	19	-	205.3	-	152-287
51	-	14	-	227.0	-	170-303
52	-	26	-	244.4	-	200-295
53	-	23	-	247.4	-	185-327
54	-	27	-	266.4	-	178-413
55	-	29	-	279.2	-	218-340
56	-	25	-	292.0	-	240-340
57	-	25	-	310.4	-	255-375
58	-	23	-	317.0	-	265-405
59	-	24	-	358.4	-	290-425
60	-	22	-	360.2	-	290-440
61	-	18	-	380.9	-	300-460
62	-	5	-	406.6	-	352-520
63	-	8	-	385.0	-	340-420
64	-	5	-	448.4	-	375-595
65	-	4	-	455.8	-	430-470
67	-	2	-	481.0	-	462-500
68	-	2	-	465.0	-	450-480
75	-	1	-	620.0	-	-
76	-	1	-	667.0	-	-

3.44 Metabolism

Metabolic rates.

Several investigators have studied the oxygen consumption of eels. Krogh (1904) found a consumption of 40, 45 and 60.5 mg/kg/h at 8°, 16° and 25°C, respectively. Wienbeck (1979) mentioned a consumption of 29.3 and 55.1 mg O_2/kg/h at 15° and 25°C, respectively. After feeding these values increased thrice: 91.1 respectively 147.5 mg O_2/kg/h. Nicol (1960) mentioned 63.4 mg O_2/kg/h at 16.5°C. Precht (1961) found for two eels kept at 18°C values varying from 49 to 67 mg O_2/kg/h. Boëtius and Boëtius (1967) studied the oxygen consumtpion of captive silver eels; at 12.5°C it amounted to 20 mg O_2/kg/h. At about 30°C the consumption was about 111 mg/kg/h after acclimation for 3 to 9 days, and about 94 mg when the acclimation period was 10 to 15 days. At a temperature of 22°–25°C, oxygen consumption was about 57 mg/kg/h. The authors concluded that respiratory rate and heart rate of the silver eel show a maximum at about 25°C.

Attention must be drawn to the statement of Geyer and Mann (1940) that fishes kept together, consume less oxygen than they would if kept separately. This opinion is in full agreement with the experiences of eel merchants, who manage to keep very many eels in tanks, provided the eels are put in gradually and not simultaneously.

Byczkowska-Smyk (1958) calculated the gill surface of a 1 kg eel to be about 9900 cm^2, which is extremely low compared with the gill surface of other fish species. Krogh (1904) had, however, previously explained this discrepancy by showing that eels respire through their skin, which provides for about 3/5 of the total oxygen uptake, made possible by a special capillary system.

Endocrine systems and hormones.

Experimental maturation of both male and female eels with simultaneous increase of gonads, growth of the eyes, atrophy of jaws, internal atrophy in the head and changes of coloration have been induced by several authors (cf. Boëtius and Boëtius, 1980; see also 3.17). Attempts at fertilization succeeded in few cases, but embryonic development ceased at the gastrula stage.

Jasinski (1961) and also Muir Evans (1940) studied the pituitary gland of the eel. The latter discovered certain changes connected with the eel's biology, including the development of the gonads.

With regard to osmotic relations, attention must be drawn to Parry's (1966) compilation about osmotic adaptation in fishes. From it some items may be mentioned here.

Most striking changes in tissue composition have been observed during an eel's life. The leptocephalus contains 94 per cent water, elvers passing into estuaries have 86 to 80% after one week in fresh water 82 per cent; the water content of muscles declines from 73 per cent in yellow eels to 63 per cent in silver eels. The decline in water content is associated with fat and nitrogen accumulation but also with an increase in electrolytes:

	Organic (g/kg water) nitrogen	fat
Elvers	25	29.2
Yellow eels	42	40.8

	Electrolytes (m-equiv./kg water) sodium	potassium	calcium	magn.	chloride
Elvers	36	670	157	16.2	19.2
Yellow eels	63	890	195	17.1	27.6

The muscles of eels in seawater, prior to the spawning migration, have shown a 10 to 15 per cent increase in electrolytes.

Integrity of the skin is important in maintaining internal stability. Impaired osmotic control results if the mucous coat is not intact as is the case with elvers. Salinity change is followed by a gradual change in blood concentration; with a grown eel 50 h is needed for the blood concentration to stabilize within the normal range.

Compared with yellow eels, silver eels show a lower cortisol level, an increased redistribution and utilization of fat, a changed carbohydrate and protein metabolism and an enhanced content of dark muscle fibres (Lewander et al., 1974).

Silver eels have been investigated especially (cf. Parry, 1966).
It appears that their alimentary canals play an important osmotic role . When filled with seawater they absorbed 18 to 14 per cent of their volume of water from the medium. This passive influx of water was greater in alimentary canals from animals adapted to seawater than in those from animals in freshwater. There is also a passive sodium efflux from the gut at a rate 16 to 35 per cent in 2 h. It is suggested that there is an initial loss of body water in the gut, followed by a loss of sodium from the gut into the blood, and then absorption of water from the gut fluid.

In the silver eel, glomerular filtration rate changed from 110.5 ml/kg/day in freshwater to less than 25 ml/kg/day in seawater; the definitive urine volumes were 84.5 and 15 ml respectively. This adaptation to a more saline environment thus involves both a change in glomerular filtrationrate and in tubular resorption.

Water and sodium chloride follow osmotic and ionic gradients. The gills of eels adapted to seawater lose sodium chloride ten times faster in seawater than in freshwater, while those of freshwater eels lose salt independently of the concentration gradient.

Adaptation to a given external medium seems to be important. Isaia and Hirano (1975) concluded that it brings about a decrease in the osmotic permeability so that water gain in fresh water or water loss in salt water is minimal.

The specific locus for salt exchange was restricted by Keys and Willmer (1932) to acidophil cells in the gill-epithelium at the bases of the lamellae. The "Keys-Willmer cells" have been subjected to an investigation carried out by van Dyck (1966). A remarkable increase in the number of Keys-Willmer cells was observed in injured eels living in seawater: the mean number of cells per lamella base increased from 3.12 to 4.79. Moreover the cells change in aspect, in size and in number during different stages in the development of the animals, when these are exposed to water of different salinities, either under natural or experimental conditions.

Sargent et al. (1978) continued the study on structure and function of chloride cells in the eel gills and on basis of their observations proposed that salt pumping in the gills stems basically from an unusually high concentration of sodium pumps delivering a very high concentration of NaCl into a specialized space between adjacent chloride cells that is essentially "open" to sea water.

3.5 Behaviour

3.51 Migrations and local movements

Migration seems to be the most important phenomenon in the life cycle of the eel. In fact all stages of eels show a more or less pronounced migration, and with the exception of the yellow-eel stage all stages are fully engaged in performing extensive migratory movements. Only the yellow eels show distinct sedentary periods, which are used for feeding and fattening.

From what is known about eels the conclusion may be safely drawn that they have a close connection with deep-sea regions. Some species have transferred their feeding area from the sea to freshwater, and these species all show migratory movements which are a logical consequence of the combination: deep-sea spawning area, strong oceanic current flowing away from that area, coastal area touched by this current and freshwater to grow up and mature in.

Apparently this combination is essential for all the migratory eel species, implying that the peculiar life histroy of the European eel shows considerable similarity to that of other species.

It is suggested that the life history of the European eel is a result of continental drift, creating a gap between America and Europe-Africa (cf. v.Ubisch, 1924). It may be noted here that the relation of all eel species with deep-sea regions may be regarded as primary, while the relation of some species with a freshwater area is secondary. In the case of continental drift, this would imply that before the drifting started a deep-sea area was already present between the continents, which has remained near the American continent.

3.511 Migratory movements of the larval or Leptocephalus stage

After tentative suggestions by various authors, among whom certainly must be mentioned both Redi and Spallanzani, who deduced that eels spawned in the sea (cf. Bertin, 1956, p. 4-7), it was Schmidt (1922, 1923) who developed a thesis on the migratory movements of the larval eel. This was based on numerous data collected by him in the Atlantic and the Mediterranean after the first larva-find in the Atlantic by him in 1904 off the Faroe Isles.

Migration starts at the spawning area which Schmidt assumed to be situated between about 22° and 30°N, and about 48° and 65°W, with the central part at a lattitude of about 26°N, coinciding with the depths of the Sargasso Sea.

Bertelsen (1967) defined the spawning area more precisely during the "Dana"-expedition of 1966. Numerous small larvae were found in April in the South-Western part of the area described by Schmidt, and only there. As no larvae were found during the preceding February cruise, he concluded that spawning begins at the end of March in this area, which is situated near the intersection of the Tropic of Cancer with the 60°W meridian.

On account of their recent investigations, Schoth and Tesch (1982) obtained results that are essentially in accordinace with Schmidt (1924), especially true when latitude is concerned. Assuming that occurrence of 7 mm larvae is congruent with the spawning area, it must be concluded that its western limit lies beyond 69°W.

The course of the larval migration may be described best in Schmidt's own words: "Spawning commences in early spring, lasting to well on in summer. The tiny larvae, 7 to 15 mm long, float in waterlayers about 200 to 300 m from the surface, in a temperature of about 20°C. The larvae grow rapidly during their first months, and in their first summer average about 25 mm in length. They now move up into the uppermost waterlayers, the great majority being found between 50 and 25 m, or at times even at the surface itself. Then they commence their journey towards the shores of Europe, aided by the eastward movement of the surface-water itself. During their first summer, they are to be found in the western Atlantic (west of 50° long, W.). By their second summer they have attained an average length of 50 to 55 mm, and the bulk are now in the central Atlantic. By the third summer, they have arrived off the coastal banks of Europe, and are now full-grown, averaging about 75 mm in length, but still retaining the compressed, leaf-shaped larval form" (Fig. 3).

Considering the frail appearance of "Lephtocephalus brevirostris", it is obvious that it leads a planktonic life, so that its distribution is determined by movements of the currents in the sea of which the Gulfstream and the North Atlantic Current are the most important.

This assumption explains the distribution during the winter months in the Mediterranean, where eel larvae have been observed as far east as the Sicilian Channel and the Straits of Messina, transported there with Atlantic water from the Straits of Gibraltar by the Mediterranean surface currents, as Schmidt already presumed in 1912 (Schmidt, 1928; Sverdrup et al., 1952).

With regard to the Atlantic journey, however, some doubt rises. Brongersma (1967) traced a case of a loggerhead turtle (Caretta caretta (L.), which stranded at the Shetlands when being just over a year old and which must have been carried over the Atlantic by the prevailing current streams in that period. Moreover, combining data on the movements of derelicts that have floated from American Atlantic waters to European coasts, an earlier worker estimated the duration of the voyage to be 13 to 17 mo. This fits in nicely with the size of the smallest turtles recorded in British waters. According to oceanographical evidence, the shortest time needed by a floating object to drift from the Florida Strait to Great Britain can be estimated at ten months, and some turtles may have completed the crossing in that time, but under less favourable circumstances the trip will take a year or even more.

This evidence, assembled by Brongersma, does not tally at first sight with Schmidt's ideas of the Atlantic crossing of the leptocephalus, and the subject therefore needs more investigation.

Latest developments in this respect are made by German scientists (cf. Tesch, 1982); e.g., Kracht (1982) found that the distribution of I and II-group eel larvae is neither in agreement with hypothetical Atlantic drift charts, nor with the assumption of distribution by either Gulf Stream or North Atlantic Current.

This conclusion is fully supported by the age determinations on larvae otoliths by van Utrecht and Holleboom (in press), who proved that eel larvae do not possess a uniform life history. As the otolith zones show the same structure as the annual zones in otoliths of Ang. rostrata (cf. Liew, 1974), the authors with fair certainty credit European glasseels with an age of 1-6 years, with a majority of 3-4. As eel larvae have been observed without exception with empty gut only, the question rises how they manage to stay alive and grow without feeding. A solution is offered by Marshall (1979), quoting Hulet (1978), who after close study of leptocephali of the bandtooth conger eel, Ariosoma balearicum suggested that before metamorphosis leptocephali derive their nutrition from dissolved and minute particulate material in the sea, and there is preliminary evidence (from tracer work) of their uptake of solutes.

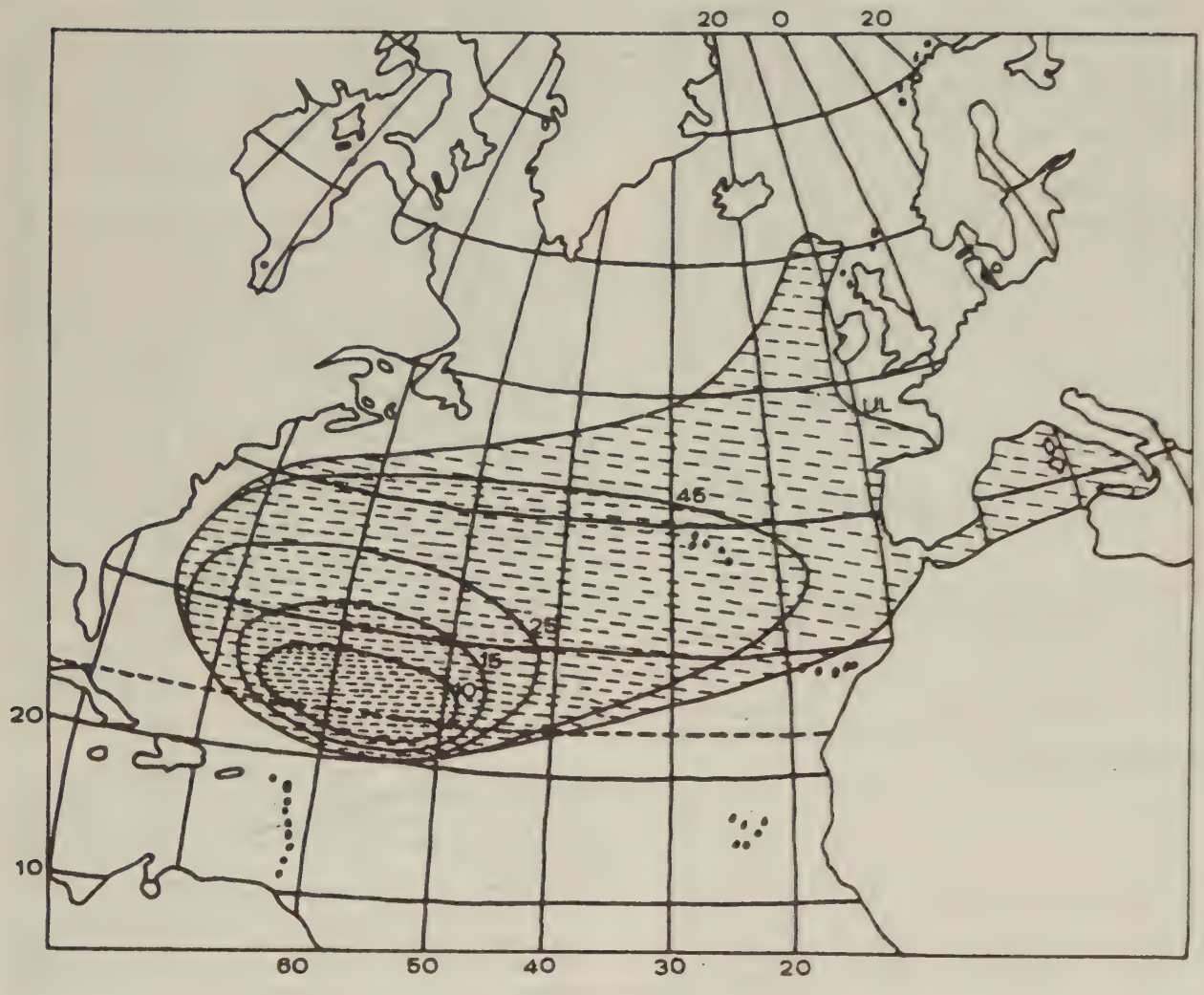

Fig. 3 Showing the supposed distribution of eel larvae in the Atlantic (after Schmidt, 1928). The lines on the dotted areas show limits of occurrence of larvae; i.e. larvae less than 10 mm have only been found up to the curve denoted by 10; u.l. indicates boundary of unmetamorfosed larvae. See also: Schoth and Tesch (1982) and Kracht (1982).

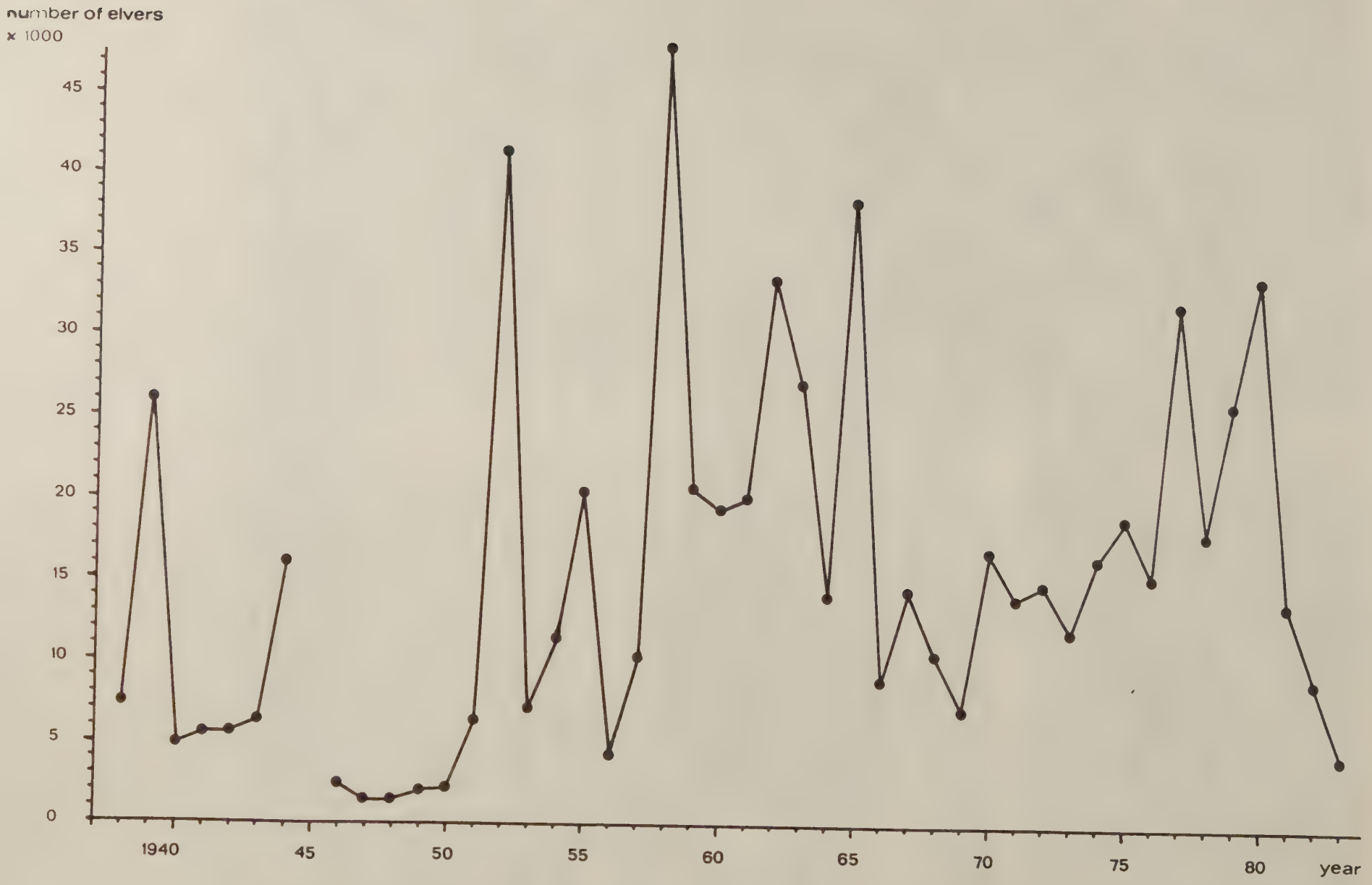

Fig. 4. Graph showing the number of glasseels, annually caught at Den Oever (Netherlands) with a dipnet at 2-hour intervals during the night

Due to the fact that several year-classes of eel larvae are on their way at sea, they sometimes are called the migratory fish "par excellence", although oceanic currents might influence their movements. When full grown, they stay in the vicinity of the 1 000-m depth line around the European continent (Schmidt, 1928). (No data about this feature in the Mediterranean are known.) Here they manage to stay and here they metamorphose, i.e., they turn into elvers in autumn. After having become elvers the migration is resumed in winter.

It is of interest to speculate about the ability of lephtocephalids to recognize the 1,000 m depth area so that they interrupt their migration and stay there for some time to metamorphose. In this respect attention may be drawn to Westenberg's idea that many pelagic teleosts are able to discern different depths. Westenberg (1952) stated that certain Indonesian fishes are able to swim parallel to a coast; they are even able to keep along a certain depth contour (as the leptocephali do). He explained this feature not as due to the surf but to the ruffled water surface sending vibrations downward which are reflected from the bottom. This will set up resonance with an average wavelength of four times the depth, so that a particular low-frequency resonance will correspond to a certain depth, which resonance should be discernable with the fish' auditory and/or lateral line system.

3.512 Elver migration

During the period between the two metamorphoses of larvae turning to elvers and elvers turning to eels, the elvers do not feed (Johansen, 1905). Consequently they dininish in size.

Grassi and Calandruccio (1897) showed with aquarium experiments that the metamorphosis of the eel larvae into elvers is accompanied by a diminution in breadth and length. The characteristic of early-season elvers being larger than the elvers arriving later is well known too. Johansen (1905) measured elvers in the North Sea and off Denmark and noticed a difference of about 6 mm between mean lengths at the start and the end of the season. Similar observations have been made by Paget (1923, see also Lübbert, 1930), Heldt and Heldt (1930), who observed a difference of 6 mm between the mean lengths of elvers, and Menzies (1936) who published graphs on the lengths of elvers reaching N. Ireland which show a decrease of almost 4 mm during the season. Menzies moreover noticed that at the end of the season the elvers are obviously thinner than before. It may be safely concluded that the process of deterioration during the metamorphic stage is progressive until the elvers start feeding again, and Schmidt (1906) put the total loss in length at 1 cm, taking about a year.

According to Bertin (1956) quantities of elvers reaching the coastline show a definite periodicity, not only yearly but also a six-yearly. All variations in the abundance of elvers in his opinion must have their origin in variations in the great waters.

Elver catches at Den Oever (Holland), however, carried out from 1938 onward in strictly the same way, do not reveal any periodicity at all. The same conclusion may be derived from catches at the river Bann (N. Ireland) and the Severn (England) (cf. Deelder, 1952), (Fig. 4).

Heermans and Van Willigen (1982), who studied data of nearly 70 000 glasseels (average length: 73 mm; minimum: 56 mm; maximum length: 92 mm) along the Dutch coast, observed a relation between water temperature, migration and body length. Normally the water temperature is about 4-5°C at beginning of the migration period. After a cold winter, the migration starts later and lasts shorter than normal; in this case the animals are taller (up to 77 mm average). After a warm winter, migration starts earlier, lasts longer; the glasseels are shorter, down to 77 mm average.

The migration of elvers has often aroused considerable interest and consequently has often been the subject of scientific study, especially in coastal waters, where investigations could be carried out most conveniently. These results, with some extrapolation, lead to a tentative hypothesis.

Because the area of metamorphosis in the Atlantic is at the edge of the continental shelf, the migration here occurs mainly in water areas under tidal influence, and for this reason one may be inclined to assume a relation between elver migration and tides. Studies carried out in the coastal waters of the North Sea have shown that elvers here use tidal movements, but one should not forget that a great many elvers migrate annually in the Mediterranean where tidal influence is practically nil. Nevertheless elvers still manage to reach areas as far as Egypt or the North of the Adriatic in winter or early spring. It is a pity that comprehensive data about migration in the Mediterranean are lacking, as in our opinion results from here may be revealing about the nature of elver migration in the open sea. In this respect the observations of Paget (1923; see also Lübert, 1930) deserve attention. He noticed that in Egypt, elver immigration occurs in two distinct waves, with some months between. This feature contrasts with the situation in Western Europe and in the Western Mediterranean, and in our opinion suggests that elvers reach Egypt via two different migration routes in the eastern part of the Mediterranean.

According to Schmidt (1906) elvers can be discovered every year in the Atlantic from September to November onward, and we may assume that elver migration starts in this period from the area of metamorphosis towards inland waters. Schmidt also produced a map of Western Europe, later completed by Walter (1910), which showed several areas and the most important months of elver immigration, although in the South Atlantic regions freshly arrived elvers might be observed the whole year round (cf. Charlon and Blanc (1982) for the French coast near the Spanish border).

The data by Schmidt and Walter can be used to calculate the migration speed at sea. The latest attempt was made by Meyer-Waarden (1965) who mentioned a value of about 7 km per day, but this cannot be more than a rough result considering the uncertainties of the beginning and end of the migration. To show this, one example may be put forward here: Schmidt (1906) mentioned immigration into the Severn (England) in February; Creutzberg (1961) and Meyer-Waarden (1965) put the Severn in the December area, while the common opinion in the Severn area is that normally elver immigration begins here in April.

Nothing conclusive is known about the start of elver migration at sea; the end period, when the elvers strike land, is strongly influenced by the water temperature (Table IV). In mild winters first elvers arrive, e.g., in Holland as early in December. Assuming the same starting time, this would lead to the conclusion that elvers are able to achieve a much higher migration speed in the sea than Meyer-Waarden found. It is hard to imagine how these tiny animals succeed in achieving such a velocity by their own strength, which consideration strengthens the assumption that elvers may use the sea currents, i.e. the tidal streams, for their transport.

As stated above, the elver migration in estuarine waters has been a subject of some studies. Deelder (1960) from 1946 to 51, and also Creutzberg (1961) from 1955 to 57, observed the phenomenon that, superimposed upon a vertical day-night rhythm, elvers swim in the upper water layers during flood tide and keep to the bottom during ebb tide, thus causing extensive inward migratory movements if flood coincides with darkness. Hence it is obvious that elvers discriminate between the

TABLE IV

The dates on which elvers were first noticed at Den Oever, Holland, in a series of years and the water-temperature of the coastal sea in front of Den Oever. (After Deelder, 1952)

	Elvers	Temp.°C		Elvers	Temp.°C		Elvers	Temp.°C		Elvers	Temp.°C
		1938			1939			1940			1941
6.III	–	5.1	22.II	–	4.1	29.III	–	4.4	14.III	–	3.9
	–	5.5		–	4.1		–	4.8		–	3.9
	–	5.6		–	4.5		–	4.6		–	4.0
	–	5.8		–	4.5		–	5.4		–	4.2
	–	6.1		–	4.6		–	5.8		–	4.1
	–	6.2		–	4.6		–	5.6		–	4.2
12.III	23	6.0	28.II	43	4.4	4.IV	83	5.8	20.III	5	4.7
		1942			1943			1944			1946
6.IV	–	4.7	27.II	–	5.1	15.III	–	4.1	5.II	–	4.2
	–	5.4		–	5.2		–	4.3		–	4.3
	–	5.3		–	5.5		–	4.6		–	4.5
	–	5.5		–	5.7		–	4.7		–	4.8
	–	5.1		–	5.9		–	4.8		–	4.7
	–	5.4		–	5.0		–	4.7		–	4.3
12.IV	2	6.0	5.III	11	5.4	21.III	3	4.7	11.II	3	4.7
		1947			1948			1949			1950
5.IV	–	4.6	11.III	–	4.5	11.II	–	4.1	3.III	–	4.7
	–	4.4		–	4.8		–	4.4		–	5.1
	–	4.4		–	5.0		–	4.3		–	5.3
	–	3.7		–	5.1		–	4.7		–	5.3
	–	4.4		–	5.3		–	4.9		–	5.0
	–	4.2		–	4.3		–	4.9		–	5.3
11.IV	5	4.8	17.III	3	5.5	17.II	6	4.7	9.III	16	5.6

two tides when migrating in an estuary. Whether, in the open sea, they let themselves be transported in a certain direction by water movements and stay near the bottom during any water movement in the reverse direction, as supposed by Creutzberg (1961), is still an open question. Such a phenomenon, however, would not form an isolated case, since De Veen (1967) showed that soles (Solea solea) discriminate between different directions of the tidal currents in the North Sea.

During the estuarine migrations, Deelder (1952, 1960) could not find a relation between elver movements and salinity or temperature gradients. With regard to temperature it is sometimes supposed that temperature differences are responsible for the migration of elvers from the sea into estuaries. The warmer water of an estuary should "attract" the elvers away from the colder sea. That this opinion is not true in all circumstances is evidenced by figures published by Postma and Verwey (1950) for the water temperature at a certain point in the North Sea, at the entrance to the Waddensea and in the Waddensea. They showed that at exactly the time when migration is most intense (March to April) the average temperature is the same at all those placed, so that there can be no attraction by warmer water in the Waddensea estuary.

In a series of well planned experiments, Creutzberg (1961) did not get satisfactory results when trying to get a relation between salinity changes and the activity of elvers; he even observed an apparent indifference towards salinity. On the other hand he could release a flood- and ebb-swimming behaviour by raising and diminishing the inland-water odour content of the water, thereby proving that the odour of inland water is a factor with which elvers discriminate between the tides in an estuary. (One cannot assume, however, that this factor exerts any activity in the open sea, so if it is proved that elvers have a tide-discriminating ability there too, it must be to another factor).

After having arrived in an estuary or an area which can be considered as estuary-like, the elvers come to a delay of their migration in which the second metamorphosis or transition takes place. The factors which define the area of transition are not yet fully known, but it may be presumed that salinity together with water-temperature are the most important.

Transition may even take place near the coast in open sea, as might be deduced from observations by Charlon and Blanc (1982) for the Atlantic, and by Lecomte-Finiger (pers. comm.) for the Mediterranean.

Creutzberg (1961) pointed out that in such a transition area elvers are carried to and fro by the tidal streams (if these are present) so that they stay in the same water mass of about 8 to 11 per mille Cl and a temperature of about 4°C and higher.

Lower temperature seems to have to be correlated with higher salinity and reverse. Deelder (1952) noticed the disappearance of elvers in a certain region during a sudden cold spell. Creutzberg (1961) noticed not only that during a cold spell elvers stopped their migration much nearer the sea than normally, viz. in an area with higher salinity, but he also made the remarkable observation that under these circumstances migration with the ebb tide might be greater than with flood tide, implying that many elvers were retreating from the brackish water. (This again is an indication of the sophisticated use which elvers make of tidal movements).

From the foregoing it is evident that the area of migration delay or transition area cannot be fixed from year to year at the same position. It is obvious that under certain conditions, especially later in the season, elvers move up as high as possible, that is just in front of barriers such as weirs or sluices. Deelder (1958, 1960) had the opportunity to observe several aspects of transition in such an area, viz. at the sluices at Den Oever, Netherlands. These observations may be discussed here in brief since the transition seems to be an important stage in the migratory life of elvers. It divides migration in the sea from that in freshwater, and apparently is necessary to convert the elvers into the necessary conditions for living in freshwater.

At this place during every elver season from 1938 onward, a haul was made with a fine meshed 1 m^2 dipnet, at intervals of two hours every night in about 5 m of water. The catches (Table V) not only gave a comparison of the numbers of elvers in this brackish area during consecutive years but also revealed some other peculiarities: e.g. that under certain conditions elvers may be present with a temperature as low as 1° or 2°C, but they mostly arrive in this area with a temperature of about 4°C, as we already learned (Table IV). One of the most important items was the activity of the elvers in the upper water layers, which also here turned out to be greatest during the night (Fig.5a & 5b). De Veen (cf. Deelder, 1952) calculated the average pattern of this nightly activity in four successive fortnights and showed that it is mainly determined by the beginning and end of dusk (Fig. 6). In the daytime the elvers bury themselves in the bottom or they retreat to much deeper water of

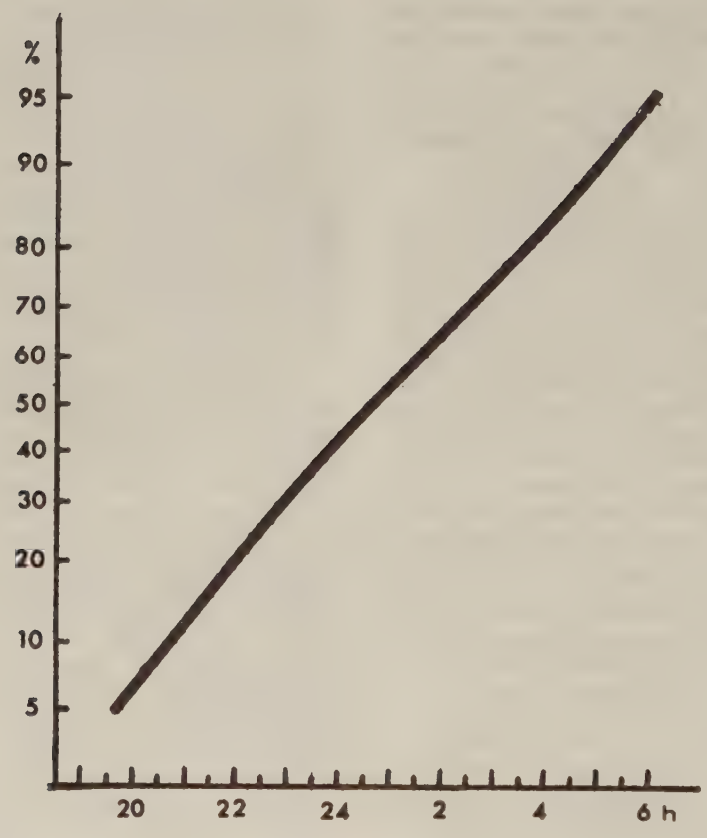

Fig. 5 The average course of the nightly glasseel activity at Den Oever (Netherlands), plotted on Gaussian paper. During the season swimming glasseels have been caught with a 1 m^2 dipnet, hauled straight from bottom to surface at 2 h intervals every night at the same place, just in front of the sluices. After Deelder, 1952 (cf. Figure 4)

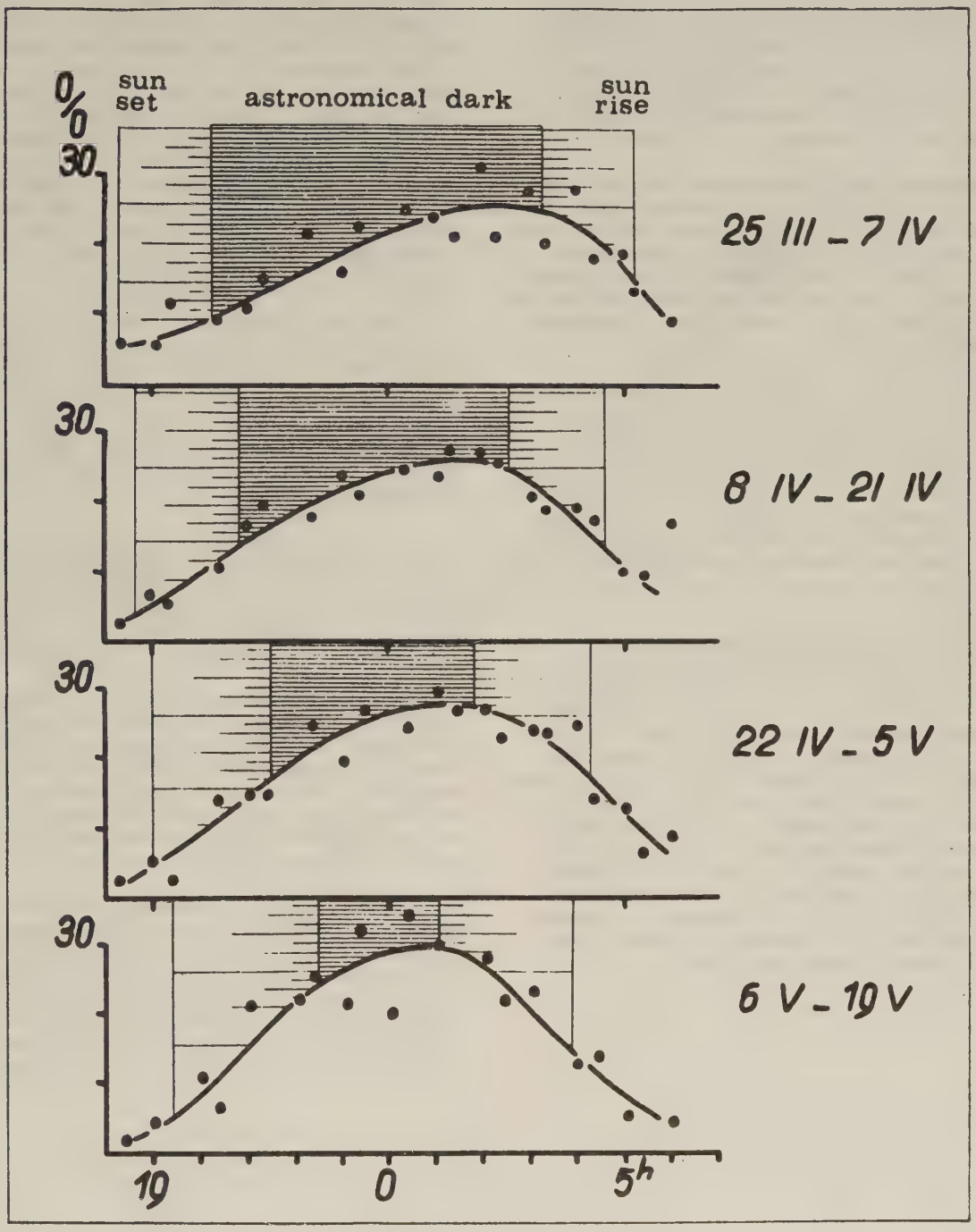

Fig. 6 The average course of the nightly elver activity at Den Oever, Holland, during four successive fortnights of the elver season. (see also Fig. 5a). After Deelder, 1952.

about 20 to 30 m if available (Deelder, 1960). In this respect the experiment of Van Heusden (1943) may be mentioned. He kept elvers in an aquarium for a long time, and by turning out and on the light in the aquarium room every day an hour earlier, he finally got an artificial night, and consequently "nightly" elver-activity in daytime, and reverse.

Comparison with catches made at the other end of the Afsluitdijk showed that no relation exists between behaviour and phases of the moon, although this is often alleged. Presumably this last opinion is influenced by local situations in which tidal movements, which are related with phases of the moon, play a decisive rôle (Deelder, 1952).

Obvious differences in conduct between newly arrived elvers and those which have been present for some time have been shown by regular observations in the transition area and lead to the conception about the temporary delay in the migration. These differences relate, among other characteristics, to vertical movements, schooling behaviour, artificial light, flowing freshwater and orientation, which phenomena have been checked by aquarium trials (Deelder, 1958, 1960).

After arrival in the estuarine area, elvers gradually develop tendencies to swim at the surface and to form schools, preferably moving along the banks. Although newly arrived elvers do not have the slightest inclination to migrate against a flow of freshwater, and even try to swim actively out of it if they get in by accident, they gradually alter to a preference for freshwater. This peculiar change-over offered an opportunity to collect data during the transition period in an aquarium about the percentage of elvers swimming against or with a flow of freshwater, thereby indicating their willingness to resume or delay their inward migration (Fig. 7).

Another method to investigate how far an elver has changed its conduct is to shine a strong light on it when it swims at the surface. Only at the end of the transition period are elvers attracted by a strong light. They are repelled by it at the beginning of the period, when they are, however, attracted by a faint light, which induces them to congregate at a small distance under the surface in the circle of light. Elver fishermen in estuaries know this phenomenon perfectly well, and for this reason use a candle or faint kerosene light to obtain the biggest catches. Deelder (1958), Elie (1979) and Cantrelle (1981) described this resp. for the Severn, Loire and Gironde.

In this connection it may be mentioned that De Veen (personal communication) made preliminary observations with a partly covered elver aquarium at the beginning of the transition period, using a movable faint kerosene lamp. He showed that elvers at that stage are attracted only by a certain light intensity and are repelled when this (small) intensity is increased or diminished.

The phenomena occurring during the transition period undoubtedly indicate that in estuarine areas the elvers stop their migration for some time and resume it after a presumably physiological change-over has taken place, which results in an adaptation to freshwater life.

This migration-stop is very conspicuous in small brooklets which flow directly into the sea. Mr. D.o'Leary (personal communication) from Ardnacrusha (Eire), stated in this respect: "We find that large numbers of elvers arrive at the junction of the brackish water and the fresh in February and usually do not enter the fresh until May or June ....".

Deelder (1960) observed that elvers, when entering artificial water-outlets, need not migrate at the surface. On the contrary, at these places they seem to prefer to migrate at the bottom. If this is not possible it will take some days more before elvers start their migration at the surface, viz. 7°C, according repeated observations by Deelder (1954a).

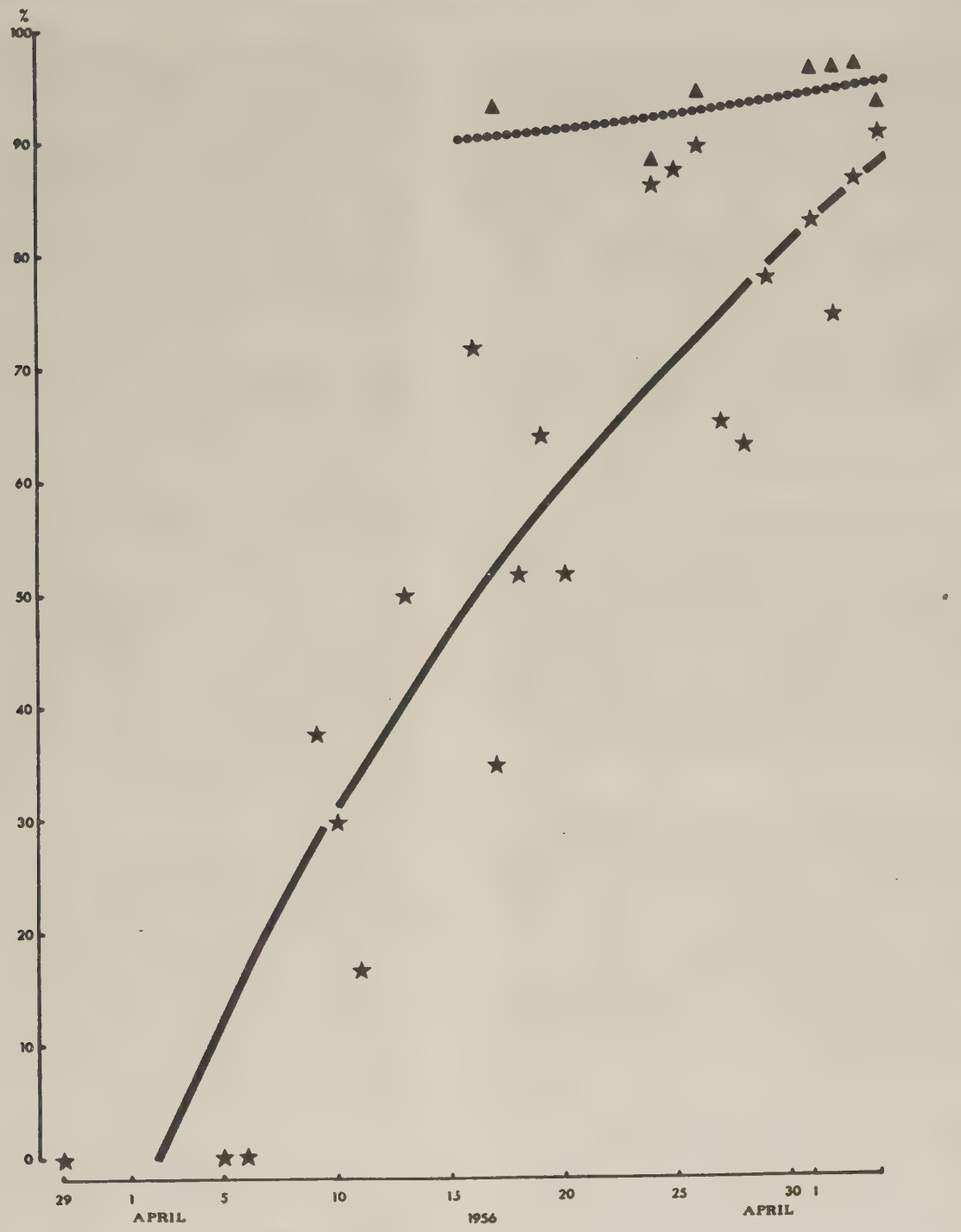

Fig. 7 Percentages of elvers staying in a small aquarium provided with a constant flow of fresh water. The lower graph refers to elvers freshly caught in sea with a dipnet. The upper graph refers to elvers caught while climbing against a freshwater-tricklet. All experiments lasted 15 minutes, except the first three of the lower series. Then the elvers had disappeared within 50, 100 and 140 seconds respectively. (After Deelder, 1958).

Once the elvers have finally arrived in a freshwater area*, their migration, if continued, occurs at the surface. The orientation of these elvers seems to be a complicated phenomenon. In completely still and pitch-black (viz. completely covered) water areas, flash-light observations of Deelder (unpublished) have disclosed that elvers are experts in orientating themselves along the banks. If such a water area is enclosed (e.g. a ship-lock) this characteristic results in an endless swimming round and round, at a speed of about 10 to 15 cm/sec. Because of the total absence of light, visual orientation must be impossible, and it is for this reason presumed that the lateral-line system plays an important rôle in the orientation. It not only enables them to locate the guiding bank, even at a distance of 1 m or more, but also to dodge impeding objects ahead. This presumption of course does not imply that visual orientation, when possible, is not applied.

Visual orientation of elvers migrating up-river might have been possible in the following situation (Deelder, unpublished). In 1955 the reconstruction of the fish- and elver-pass of the Meuse-weir at Lith, Holland, was completed. Elvers, which had climbed the elver-pass successfully, either chose to follow the riverbank at their right side or the concrete dam between the elver-pass and the weir at their left side. (Obviously the riverbank at the right was too far away (2 m) to be perceived by the last group).

The result was that at the end of the dam all elvers turned along it and consequently then swam towards the weir with its heavy overflow, which swept the elvers downstream again. To prevent this unintended development a screen had to be built, running from the dam towards the riverbank for a distance of about 20 cm. The elvers now followed first the dam, then the screen (still at their left side) and at the end of the screen picked up at their right side the riverbank, which was duly followed upstream together with their fellows from which they had recently separated.

A roughly similar situation, viz. at the underside of the Elbweir at Geesthacht, has been depicted by Tesch (1965).

In natural circumstances continued migration of elvers takes place mostly in rivers and may cover considerable distances. In Holland surface-migrating elvers have been observed at a distance of 120 km from the sea (Deelder, 1960), which area, however, was still influenced by tidal movements, so the elvers might have benefitted from flood-tides.

Because of their conspicuousness, not least at obstacles which have to be surmounted, schools of elvers always attract much attention. Some vivid descriptions have been given, including that by v.Siebold (1863), and many attempts have been made to correlate their appearances with external factors. An elver school is obviously the final result of a simultaneous responding of masses of elvers to external influences within the estuary, whereas the guiding (river-) bank acts as a concentrating factor. A study of a sighted elver school should therefore start from the transition area onward.

Statistical data on elver movements at the Herbrum-weir in the river Ems have been analysed by Meyer and Kühl (1952 to 53). They concluded that the phase of the moon, air temperature, air pressure, weather conditions, salinity and water temperature are all without influence on the migration, although at the beginning of the migration season the water temperature must be of decisive importance. From what we have learned above, it is obvious that elvers require a certain minimum temperature to migrate to inland water areas; this, according to Schmeidler (1957, 1963), is 9°C for the first few, although 10°C seems to be necessary to start full-scale migration.

According to Meyer and Kühl (1952 to 53) full-scale elver migration only occurs at night and especially when the tide is rising; 1 to 2 h after highwater the migration stops. They calculated that the migration speed in the Ems is about 2.2 to 2.5 km/h, i.e. 55 to 70 cm/sec. This high value of course refers to the earth and must be mainly the result of tidal water movement, which feature gives us a clue how to explain the start of the elver immigration.

It is commonly known that immigrating elvers are aware of counter-currents. The stronger the counter-current, the more elvers are inclined to swim close to the bank or even stop migrating at all, hiding themselves between stones, weeds and so on, until the counter-current is over. They then resume their original direction, which they keep once they have started their inward migration.

* It must be borne in mind that the term "freshwater" is used here solely to distinguish the invaded water area from the sea, without referring in the least to the salinity. In this respect we must remember that elver immigration may also occur into highly brackish or even saltwater areas, e.g. the lake of Tunis (Heldt, 1928; Heldt and Heldt, 1929). Such knowledge, combined with that of the results of Creutzberg's experiments (1961), strongly supports the idea that it is not the salinity but the odour of the water which influences the inward migration of the elvers.

Moreover we have seen that elver activity increases considerably after sunset and that freshwater in a river mouth (of which the temperature has attained at least the necessary minimal value) occurs during ebb-tide, it stimulates all those elvers which are ripe for inward migration to rise to the surface during the next night and start their migration upstream as the current gradually subsides, i.e. when the water level is rising. In doing so the elvers seek the vicinity of a riverbank for guidance, thus creating the well-known huge schools of elvers, which profit from the upwardly directed water-surge.

In this respect it may be noted here that Tesch (1965), who studied elver behaviour in estuaries of rivers in Germany, noticed most elver schools after nights when high-water at the upper boundary of the tidal flow occurred at midnight. He observed moreover that elvers may start their migration even in daylight, when the ebb occurs in the early morning. This migration breaks off during the afternoon.

From what has been discussed above, one gets the impression that the orientation of elvers is solely based on one of the banks of the water-area concerned. That this impression is not quite true, however, has been proved by Neubaur (1933) whose observations indicate that elvers are well able to keep a certain direction for some time, notwithstanding the disappearance of the guiding bank. This may be due to the outflow of sidewaters from the water in which the migration takes place or to tributaries joining it. Thus the elvers have to cross these branches to pick up the bank which they previously followed. Neubaur observed that even great drops in salinity need not divert the elvers from their original course although afterwards the elvers have to swim into water with higher salinity again.

According to this author elver-orientation may be explained by assuming that elvers smell the odour of the water in which they swim and that they follow their original course if a joining stream does not smell as attractively. Neubaur's assumptions were completely confirmed by Creutzberg (1961).

Finally we must draw attention to the phenomenon that, once the elvers are on the move, they nevertheless stop when the temperature becomes too low. This is especially conspicuous when elvers come out of the water and climb a wet area. Menzies (1936) observed at the Bann weirs that elvers stop mounting the elver-passes during frosty nights or with cold northerly winds. No matter how great the elver run might be, if the wind moves to the north, they immediately disappear from the passes and the run stops.

At the French Mediterranean coast northerly winds on the contrary exert a stimulating influence on the elver-immigration into the étangs (Finiger, 1976; Finiger (Lecomte), 1983). Due to these winds an outward superficial waterflow is created into the Mediterranean, arousing the elvers being present there in their transition area.

3.513 Eel migration

Eels, i.e. the feeding and fully pigmented animals into which elvers turn, may also show migratory movements, of which those performed in the summer seem to be of great biological importance as they are responsible for the occupation of water areas far from the sea. This statement does not imply of course that all eels migrate in summer. This is clearly demonstrated by the overcrowded stocks of slow-growing eels in river mouths, which in some cases (e.g. in Germany and Holland) gave rise to full-scale fishing, for transporting and releasing in other waters for stocking purposes.

The summer-migration may occur from estuaries up to the sources of rivers and is most conspicuous at the eel-passes alongside weirs. Moving upstream, the migrating eels show an increase in average size, and consequently in age.

In this respect Trybom and Schneider's (1908) remarks may be mentioned about summer migration in the Baltic, which can be considered as a big river-estuary with several tributaries*. According to these authors the phenomenon of increase in average size in an eastward direction is obvious. They mention the results of Nyström who measured 1,000 eels at the Trollhättanfall (Göta Alv) in Southern Sweden and who found lengths varying between 8 and 65 cm, with a majority between 20 and 30 cm. The following table is based on these data and others given by Nordqvist (1917, cf. Wulff, 1921).

* It must be stressed that the immigration into waters around the Baltic should not be compared with that in the Mediterranean, although this has been done sometimes (cf. d'Ancona, 1958). The summer migratory movements in the Baltic area are carried out by eels, no matter what size they are. On the contrary, immigration into Mediterranean countries is carried out by elvers, fulfilling their non-stop trip from the area of metamorphosis toward the inland feeding region. As eels and elvers form two different groups with strongly diverging characteristics, any comparison between migration of Baltic eels and Mediterranean elvers must be rejected.

	Number	Average age	Average length	Average weight
Trollhättan (Göta Ä)	183	3.7 year	25.7 cm	25.7 g
Motala near Norrköping	114	5.5	30.4	34.3
Älvkarleby (Dal Ä)	127	6.3	36.2	49.7

In Finland, immigrating eels are also big. Examples are given by Trybom and Schneider (1908) who quoted measurements of eels from the Kumo-elf, carried out by Nordqvist; the lengths varied between 31 and 54 cm, with the majority between 36 and 43 cm.

It is not known what part of the local eel population participates in the summer migration. Observations of Mann (1963) at the Geesthacht-weir in the Elbe showed that the summer migration may occur from the beginning of April till late autumn (even till November-December), so it is quite probable that a considerable proportion of a local eel population may be on the move during some period of the "summer".

Certain observations give the impression that summer migratory movements can only take place against a flow of water. Thus, in still waters, of which there are so many in the low countries, a distinct directed summer migration starts only if considerable amounts of water from another area are discharged into it.

In some Dutch "polders" (e.g. reclaimed lakes in which the water is kept artificially at a constant level) water is introduced in summertime to compensate for evaporation, while the excess of water is pumped out at another place. The peculiar observation can then be made that at the site of water discharge eels try to invade the polder against the outflow and "polder eels" try to get out of it by swimming against the inflowing water.

Preliminary experiments showed that an outflow without turbulence failed to attract eels during summer migration time. To attract eels by turbulent water, a simple apparatus may be used, which is also effective in guiding elvers (cf. Deelder, 1958), but it must be stressed that water must be used from another natural area.

From what is known with elvers, it is tempting to credit the water-odour with influence in relation to the summer migration. It is hard, however, to explain the upstream migration in rivers of which one has to assume that their consistency does not change noticeably in a short time.

With regard to the influence of temperature and light, more consistent data are known. Sörensen (1950) mentioned that at the Trollhättan catching station, from 1919 to 1950 no appreciable numbers of small eels were noticed when the water temperature had not reached 15°C. Moreover he concluded from his experiments that larger eels show less temperature sensitivity than small eels, and activity is decreased by low water temperatures.

Mann (1963), who studied eel migration at the Geesthachtweir in the Elbe, concluded that eels, the majority with a length between 17 and 22 cm, started their summer migration at a water temperature of 8 to 9°C. He moreover noticed a considerable increase in migration intensity when the water temperature was high (about 22°C), and a decrease when the temperature dropped. Mann (1961) also noticed a distinctly higher migration intensity during the night than during daylight, a conclusion which Sörensen (1950) had earlier reached from the outcome of his experiments. This latter author remarked, moreover, that smaller eels are less inhibited by light than larger ones, and thus are more inclined to continue their upstream movement in daylight. As such a migration may occur in huge numbers at the surface of rivers, this phenomenon does not fail to attract attention (cf. v.Siebold, 1863).

Lübbert (1923) described an eel school migrating in the Elbe. By close examination he concluded that this school had a length of at least 10 to 12 km, and a width of 1 m or more. Although the depth of the dense school was unknown it was clear that the total number of eels must have been several billions.

Besides the summer migration, eels also carry out other migratory movements, some of which may be briefly mentioned here. In spring and autumn eels may migrate between their feeding and hibernation grounds. Fishermen who are aware of this habit try to profit from it.

Another well directed movement may occur in spring towards the spawning places of coarse fishes to prey on the spawn. Again fishermen are the main witnesses of this phenomenon, and, like the migration mentioned above, it cannot be assessed properly from a scientific standpoint since no adequate data are known.

Thirdly, short diurnal migrations in estuaries seem to take place between resting places and feeding grounds. Koendzinsj (1958) demonstrated such a migration by putting a number of longlines with baited hooks, 1 to 1.5 km from the mouth of a river flowing into the Gulf of Riga. Observations covering 20 nights showed that in the evening most eels, with empty intestines, were caught by the upstream lines; at sunrise most eels were caught by the downstream lines, their stomachs filled with a crustacean species living in the sea.

Although the following subject does not belong exactly to the chapter "migration", it may best be discussed here, since it deals

with the ability of eels to proceed straight forward towards a certain area when liberated after displacement.

In this respect the marking experiments of Mann (1965) must be mentioned. He proved that non-migrating eels, living in a river, tend to stay in their home range of about 40 km length and return to it if they are transplanted.

Tesch (1967) greatly extended these experiments by tagging eels and releasing them in the Heligoland Bight. Some of his eels homed from distances of 180 km. Moreover the eels demonstrated a high ability to find small areas, such as the rocks of Heligoland (amounting only to a few km^2), from far away places like Cuxhaven and the island of Föhr, at distances of over 60 and 70 km. According to Tesch's calculations, his eels demonstrated an orientation with an accuracy within 5°. Finally Tesch recorded in two cases a minimum speed of 1 and 3 km/hour respectively.

Deelder and Tesch (1970) transplanted about 2 800 tagged eels and observed that even over displacement distances exceeding 133 km a fair number of eels were recaptured on routes pointing toward the home area. Single eels returned over a range of more than 200 km. Moreover Tesch (1970) was able to demonstrate that eels need not use their olfactory system for homing, nor do they need salinity or other factors, as, e.g., temperature and light, as orientation clues.

In agreement with persistent rumours, eels are able to discover the nearest water area when liberated on land, even at relatively great distances. In this respect Schäffer (1919) made several experiments in the water-land area south of Stockholm; his results were rather remarkable. Even when he transported the eels over relatively great distances, many hundreds of meters, and over hills, they still were able to locate the nearest water surface immediately after liberation, even when the wind was blowing from them towards the water. During these experiments Schäffer's attention was drawn twice by his eels to another water-course nearer than that he originally thought to be the nearest.

Presuming the ability of eels to recognize water from a great distance, no data are available about the factors or senses which makes this possible. However, with regard to their tendency to change from time to time water for moist land (Bergmann, 1970) it is obvious that this ability is of paramount interest for their survival.

3.514 Silvereel migration

Because of its great economic importance, the migration of the silver eel has always attracted a big amount of interest by many scientists.

The migration season may well extend over several months, mostly during the second half of the year (Fig. 8a & b, Deelder, 1954), but in fact migrating silver eels can be observed somewhere the whole year round.

In the low countries of north-western Europe the migration may start in June and already be in full swing in July. In some small water areas, this month may even be the peak of the season (Deelder, 1957), but this is exceptional. In most regions the peak of migration falls more towards the end of the year, e.g. October to November. This characteristic is also discernable under laboratory conditions; e.g. Boëtius (1967) demonstrated a pronounced autumn maximum of activity during a nine-month aquarium experiment, in addition to a spring maximum of activity (Fig. 9). This last item may be related to the phenomenon that silver eels may interrupt their autumn migration and resume it afterwards. Cold spells or freezing periods immediately interrupt the migration, which may start again even well into the next year, up to and even including May. A delay of similar duration may occur in small Danish brooks after a dry summer (Jacobsen and Johansen, 1922).

The attention must be drawn here to the phenomenon that sexual segregation may be observed during the autumn migration. E.g. Meyer (1938) and Nolte (1938) both discussed the fact, well-known among Rügen-fishermen, that relatively many more females migrate at the end of the season than at the beginning. According to Nolte the percentage of big eels (females) caught at Rügen in 1936 increased gradually from 39 in the first 10 days of September to 90 in December. Deelder (unpublished) observed an analogous phenomenon in catches if IJsselmeer silver eels, with no big eels in August 1964 and 11.0, 25.7, 46.5 and 60.0 per cent during the next months.

The average size of male silver eels may also change during the autumn migration. In that case the largest ones travel first. E.g. Deelder (unpublished) measured male silver eels in 1960 and observed an average length of 36.0, 35.5, 34.0 and 33.0 cm in July and subsequent months.

Safe conclusions about the daily rhythm of the migration can be drawn from fishermen's catches, showing that it is limited to the night. As a result of his experiments, Bräutigam (1961) was able to define the limits more closely and stated that the daily migration of silver eels in freshwater (unfavourable conditions absent) occurs almost entirely in the hours between sunset and midnight. With circumstances favourable to eel migration, Bräutigam observed that the main daily migration even concluded in the first period of nightly darkness, frequently in less than an hour.

The intensity of migration of silver eels may show distinct peaks, even of considerable magnitude. We may conclude from what is known now that these peaks are the result of a typical ethological occurrence, evoked by the combination of an internal migration-urge and external impulses. As will be discussed below, these impulses may be of different character and strength.

It may be noted that, with a sequence of external impulses at short intervals, the last

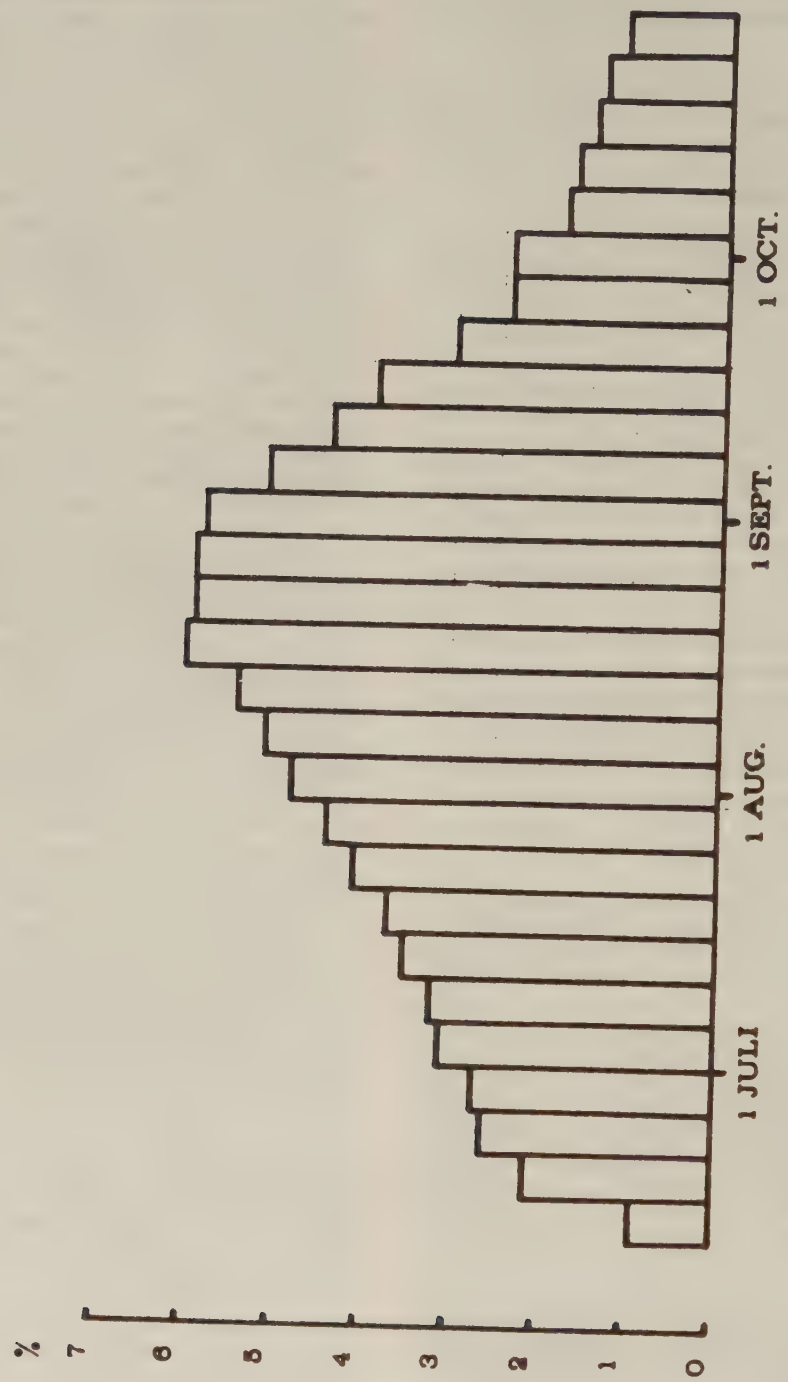

Fig. 8a The average catch of silver eels in Dutch canals by 5-day periods, from 1947 to 1952, expressed as percentages of the total catch. (After Deelder, 1954).

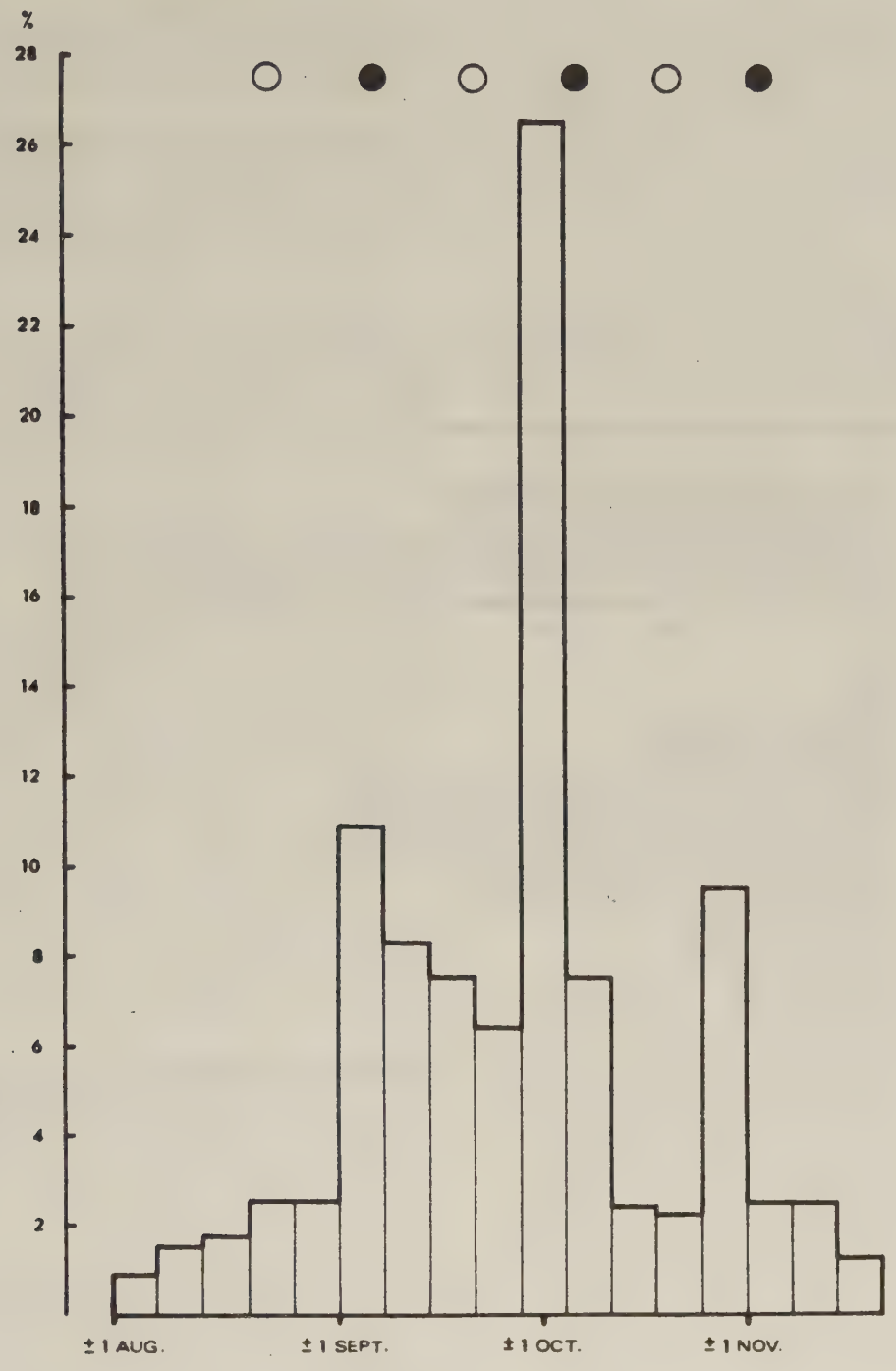

Fig. 8b Average weekly catch-percentage of silver eels in the IJsselmeer in the years 1950 and 1951; also showing periods of new and full moon. (See also Fig. 10).

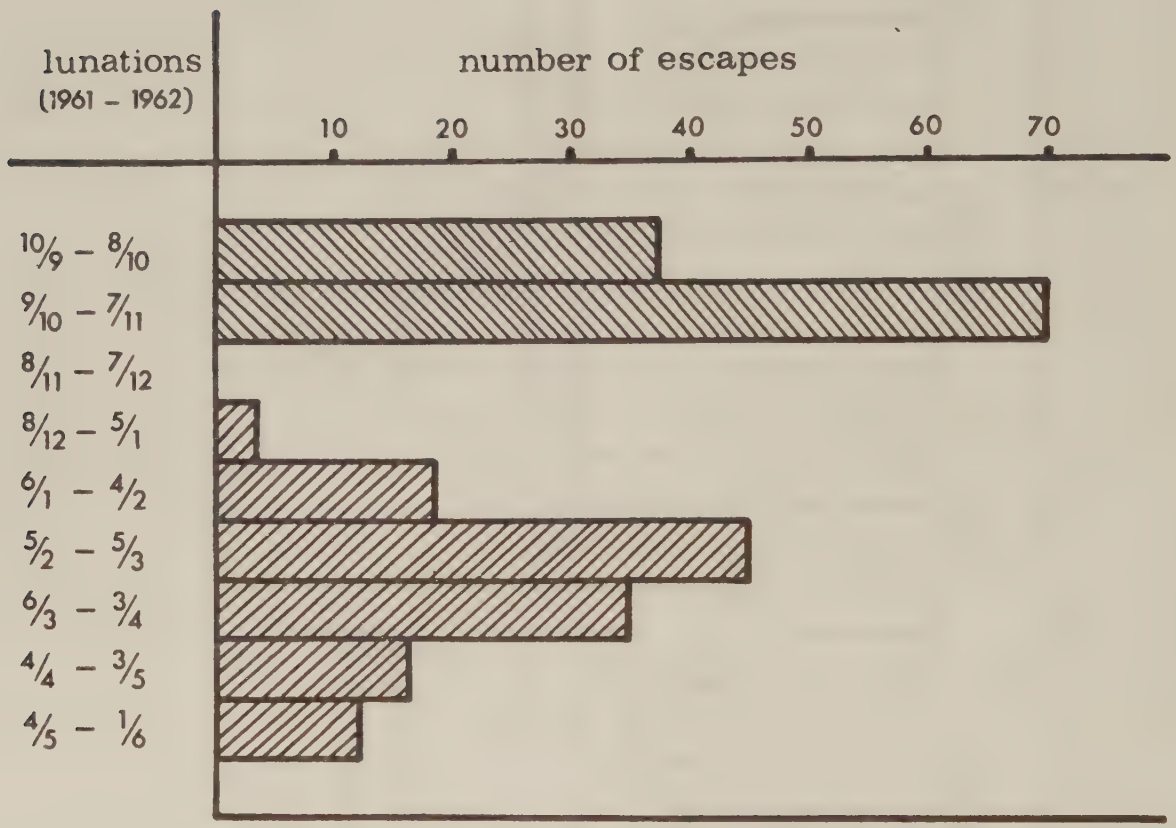

Fig. 9 Graph showing the escape-activity of aquarium-held silver eels per lunation through the total period of experiment. (After Boëtius, 1967).

impulses of course do not release the same intensity of migration as the first one, because most silver eels ready to migrate leave the area when the first impulses are received.

Not much can be said about the behaviour of migrating silver eels, largely due to the shyness of the animal. Lowe (1952) watched several migrating silver eels in an English brook and noticed that they swam head-first downstream along the bottom.

Deelder (unpublished) observed the behaviour of silver eels in a big aquarium during the night and was astonished by their apparent clumsiness. With slow snake-like movements, their round pectorals wide-spread, they seemed to "glide" lazily through the water, giving the impression that all movements are fulfilled with as small an effort as possible.

Factors affecting the intensity of migration

a) Depth

Study of regular catches of silver eels in different regions reveals the remarkable fact that shallow waters coincide with an early summer migration, while deep waters have an obvious retarding effect. Deelder (1957) mentioned several examples, including a striking one of two shallow canals in Holland leading to and from the small lake "Amstelmeer", which has depths of 10 m and more. In 1954 the percentage catches during the months July to October in the first canal were: 22, 56, 19 and 3, thus demonstrating a distinct majority in August. In the meantime the percentage catches in the second canal, through which the former silver eels had to pass too, were: 0, 0, 6 and 94 per cent, i.e. with a migration peak fully two months later.

Instances of this phenomenon have been found for more regions and invariably lead to the conclusion that deep-water areas tend to hold up migrating silver eels for one or two months, whereas shallow waters are cleared of silver eels at the beginning of the migration season.

Trapping experiments, e.g. carried out by Lowe (1952) in England, lead to the conclusion that silver eels congregate near the outflow of a lake and there await a stimulus (e.g. a "flood") to migrate further. This tallies well with Frost's observation (1950) that silver eels evidently congregate near the outflow from Lough Neagh (N. Ireland) before migrating on and thus give rise to illicit seine-fishing.

b) Moon

One of the best-known relations, mentioned by nearly everybody dealing with the migration of silver eels, scientists as well as fishermen, is that exerted by the moon. For example, Meyer (1938) and Nolte (1938), who published extensive data about silver eel catches at Rügen in the Baltic, mentioned that the best catches of silver eels are made in periods between the last and first quarters of the moon. Frost (1950) and Lowe (1952) also mentioned moonlight as affecting the numbers of silver eels migrating in the British Isles.

Jens (1952 to 1953), and independently of him Deelder (1953, 1954), analysed statistically the relation between the phase of the moon and silver eel catches, the former of the upper-Rhine and the Baltic, the latter of Dutch inland waters. Both authors agree that the best catches are made around the last quarter of the moon (Fig. 10 and Table VI).

The last quarter is that part of the lunar month during which moonlight fails early in the night. As according to Bräutigam (1961) and others, the migration of silver eels occurs only between sunset and midnight, it is tempting to assume that it is the absence of moonlight then which stimulates the migration.

According to Jens (1952 to 1953), however, the moon's influence is certainly not exerted through its light intensity. He based his opinion on the results of his study of the catches of silver eels in the river Rhine on cloudy nights. They have been classified according to the phase of moon and averages have been computed which cover a whole lunar period. Since they still exhibit a lunar rhythm, Jens inferred that moonlight has no effect.

This deduction might not be correct. An eel is subject to the influence of moonlight throughout its life, hence we must consider the possibility that silver eels have become fully familiar with the lunar cycle. For this reason one may not assume that the lunar effect does not assert itself because of a temporarily clouded sky and invisible moon. It might be supposed that direct moonlight may set up an inner rhythm during the eel's life span, which finally operates whether moonlight is present or not, as is the case with other animals (Korringa, 1947).

It must be mentioned here, however, that the moon's effect does not appear to be felt everywhere at the same time. According to Jen's data (1952 to 1953) the height of the migration in the Upper Rhine occurs distinctly before the time of the moon's last quarter, while in the Baltic (Jens) and in Holland (Deelder) it takes place after the last quarter. No explanation for this phenomenon has been found up till now. In the Upper Rhine the eels are all females, whereas in the other regions mentioned males are very abundant or even

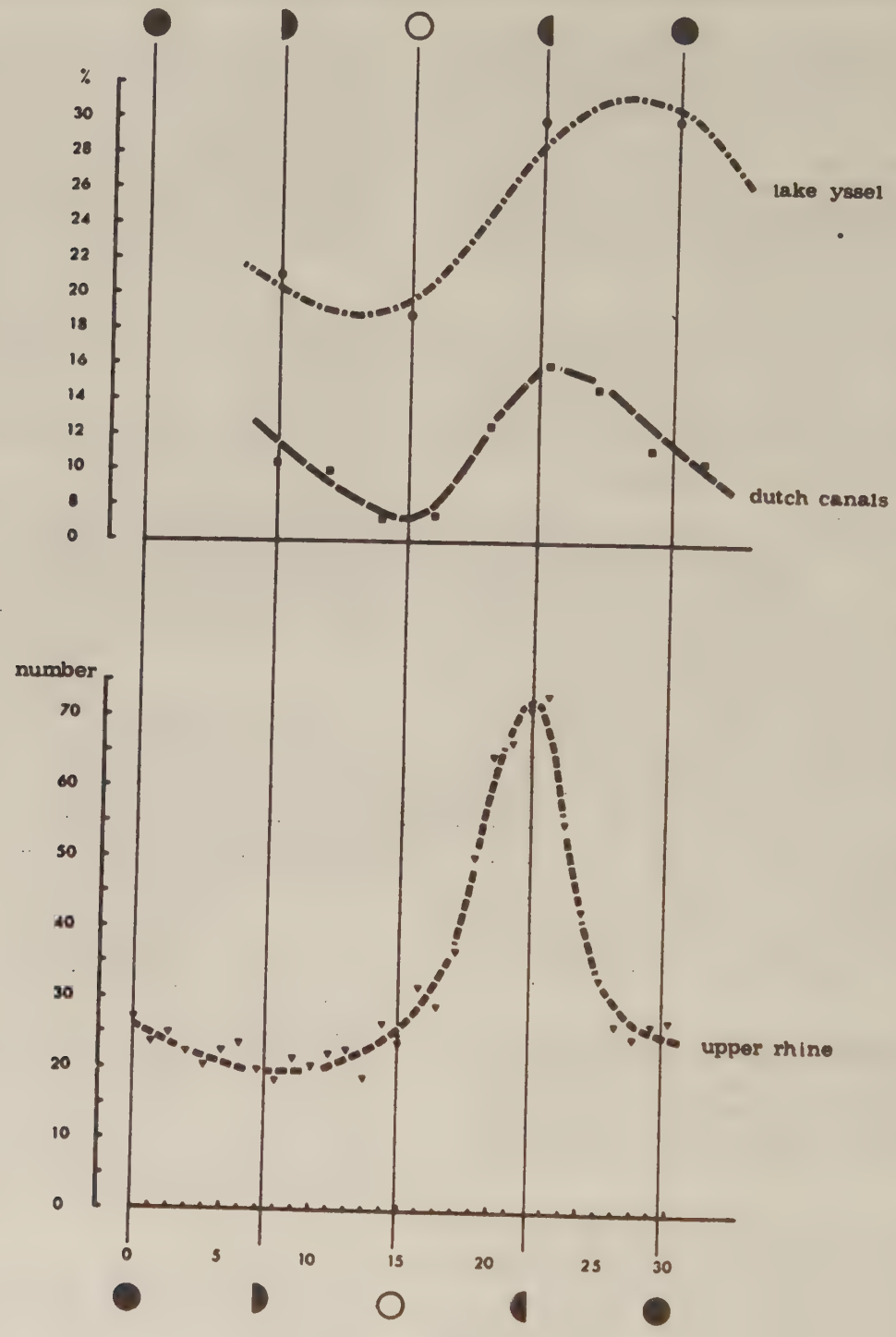

Fig. 10 Average fisherman's catch of silver eels per autumnal lunation in Holland and in the Upper-Rhine. (After Deelder, 1954, and Jens, 1952/53).

TABLE VI

Escape activity in relation to the phases of the moon. (After Boëtius, 1967)

	Total exp. period escape-number	% of total	Period 10.IX- 8.XI escape-number	% of total	Period x.XII-2.VI escape-number	% of total
New moon	21	9	7	7	14	11
First quarter	31	13	12	11	19	15
Full moon	42	18	17	16	25	19
Last quarter	144	61	71	66	73	55

predominate; the possibility therefore exists that the phenomenon is caused by difference of sex.

c) Waterflow and/or - level

According to fishermen, an increase in waterflow may be associated with an increase in numbers of migrating silver eels. This opinion seems to differ from that of several scientists. Jens (1952 to 53) examined the relation between the catch of silver eels and the water level in the river Rhine (Fig. 11) and drew the conclusion that most eels are caught when the water level is highest. He also mentioned better catches with rising water level. Frost (1950), and Lowe (1952) also concluded for British rivers that an increase in catch usually coincides with a rise in water level.

In our opinion, however, it is not so much the high water level as the increased flow which encourages the eel to migrate. In this connection the many Dutch "polders" must be mentioned, low-lying areas enclosed by a dike, in which the water is kept at a constant level by pumps (formerly by windmills). As soon as these begin to eject water out of the polder, the water in the polder canals starts to flow towards the pumps. While the flow occurs larger catches of silver eels are made, which feature suggests that the silver eels are stimulated into migration by the flow, since the water level remains approximately the same or is even falling (Bicker Caarten, 1946). Obviously then it is the increased flow, which in rivers necessarily coincides with a rise in water level, which acts as a stimulating factor. In this respect it is important to know that Frost (1950) plotted silver eel catches in the river Bann (N. Ireland) against the amount of water flow over a weir and showed a good relation between increase in catch and increase in the amount of water passing.

d) Turbidity

Frost (1950) mentioned the reports of Bann fishermen that discoloration of the Bann (N. Ireland), e.g. by peat bog drainage, makes fishing better than under the same conditions without turbidity.

e) Depression-generated microseisms

Nolte (1938) studied diaries of Rügen fishermen and concluded that during dark stormy nights unusually rich catches could be made, although favourable wind directions obviously were not necessary.

Frost (1950) and Lowe (1952) also stated that on stormy nights silver eels in British rivers may migrate in large numbers. Deelder (1954) studied catch results in Dutch canals during the period 1947 to 52 and distinguished 28 cases of distinct increase in catch; this offered an opportunity to check the extent to which weather conditions may be held responsible for the occurrence. He learned that in every case, without exception, weather conditions over the Netherlands were governed by a depression in the vicinity. Examination of the particular factors commonly associated with a depression, e.g. wind strength and direction, air temperature, barometric pressure, cloudiness and precipitation, failed to show any which might be acting as a stimulus to migration. In six cases the prevailing weather conditions were in no way favourable to eel migration in the opinion of fisheries experts.

One factor, however, was discovered which may provide the stimulus, viz. microseisms. These are vibrations of the ground and are frequently caused by depressions at sea (Scholte, 1954). The vibrations are probably set up by the forces exerted on the sea-bottom by the

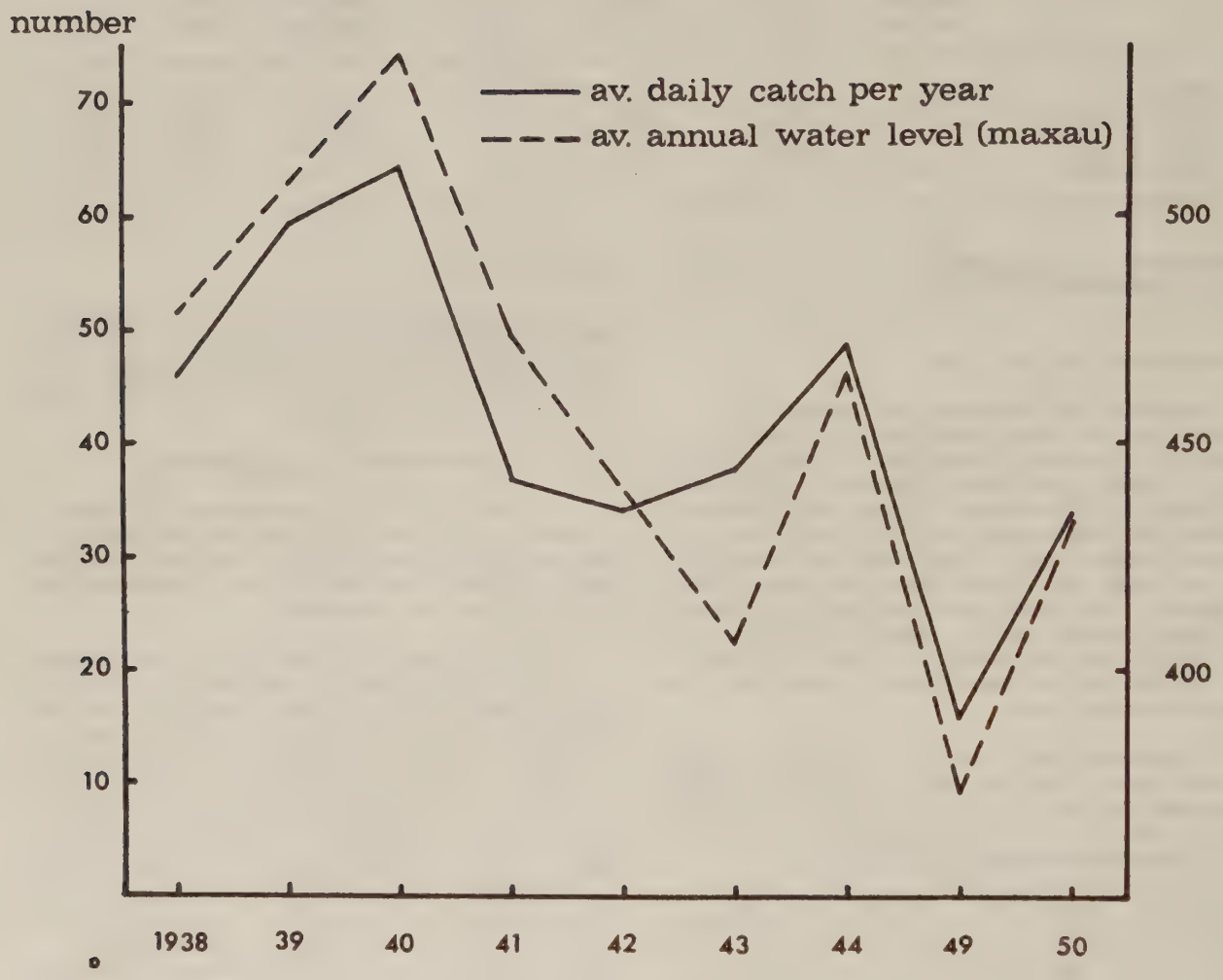

Fig. 11 Annual average daily catch of silver eels per Upper-Rhine fisherman compared with average annual Rhine-level at Maxau, Germany. (After Jens, 1952/53).

high waves at the centre of the depression. From there they pass through the ground at a speed of several kilometres per second. They may be resolved into three components, two horizontal and one vertical, and may last for hours.

The period of the vertical component depends on the depth of the sea, the amplitude depends on the intensity of the depression and varies in Holland between 1 and 20 μ. Depressions in the Atlantic produce microseisms mainly with periods of 6 to 8 sec; with those over the North Sea periods are noticeably shorter (Fig. 12). Since there is a sharp division between the depths of the Atlantic Ocean (1,000 to 4,000 m) and those of the continental shelf (100 to 200 m), the corresponding microseisms in Western Europe can be put into two fairly distinct groups. Microseisms with a period of 4 sec and amplitude of 7 μ cause pressure fluctuations at the base of a 10 m water column of a magnitude of 2 dynes/cm^2, i.e. 0,002 millibar.

Careful study of the available data, covering a series of about 1,000 fishing days, revealed the remarkable fact that the numbers of migrating silver eels only rise sharply, without exception, after the occurrence of microseisms with a 3- sec period, caused by depressions over the North Sea and the English Channel.

The assumed relation between microseisms and migratory stimulation implies that captive silver eels should be motivated by microseisms too. In this regard the laboratory observations of Lowe (1952) must certainly be mentioned; her indoor aquarium-kept silver eels showed considerably increased activity only on those nights on which free living silver eels migrated in large numbers. In Deelder's opinion microseisms, generated in the relatively shallow Irish Sea, must be held responsible for this phenomenon.

Muir Evans (1940) stated that in Norfolk it was the custom for eel catchers to keep a few silver eels in a perforated trunk in the water. They did not put down their eel-setts unless these eels became restless, which was a signal that the other eels were running and that the night was favourable for a good catch.

f) Seawater

According to fishermen's allegations silver eels staying in freshwater are greatly stimulated by inflowing seawater. This phenomenon is known especially from lagoons and river mouths around the Mediterranean. Since inflowing seawater occurs at those places mainly during gales, the question remains if the silver eels are activated by these storms (see section e. above), by the seawater or by both phenomena.

The available data, however, point to the assumption that silver eels in freshwater are not uninfluenced by seawater. Those silver eels tend to swim against a seawater flow (again according to fishermen) which conduct is in contrast to that towards a freshwater flow. (See section c, and under). Moreover, captured silver eels, transported in a fish-well show high activity when transferred to seawater.

Fishermen in Holland are of opinion that seawater, artificially introduced so that it creeps over the bottom, stimulates the migration. As in this case depression-influence does not exist, one might indeed presume that inflowing seawater exerts a stimulating effect.

Factors influencing the migration route

a) Flow direction

Silver eels migrating in inland waters where there is no obstruction tend to swim with the current if there is one. Deelder (1953) showed that the direction of migration changes with the flow when he compared catch-results on both sides of a net barring a canal with an alternating weak flow.

As we already learned the silver eel's migration activity is greatly stimulated by an increase of the water current. The biological consequence of both phenomena obviously is that migrating silver eels which have themselves been guided by a waterflow invariably reach the sea and moreover do so with the least effort.

During their migration silver eels indeed try to profit from water movements, which is clearly demonstrated by the "schokkerfishermen" at the N.W. European rivers, e.g. the Rhine. They are keen to get the mouths of their funnel-shaped nets at the line of greatest flow, and, according to them, the catch here is greater than could be expected in relation to the flow-rate. As the line of greatest flow in rivers mostly coincides with the line of greatest depth, it follows that one certainly has to bar this region if one intends to catch silver eels in rivers.

As already discussed, the tendency to swim with the freshwater current is reversed when seawater flows into the freshwater region.

b) Wind direction

The course of the silver eel migration in broad water stretches, e.g. lakes, is obviously influenced by the direction of the wind. Frost (1950) mentioned that a strong southerly

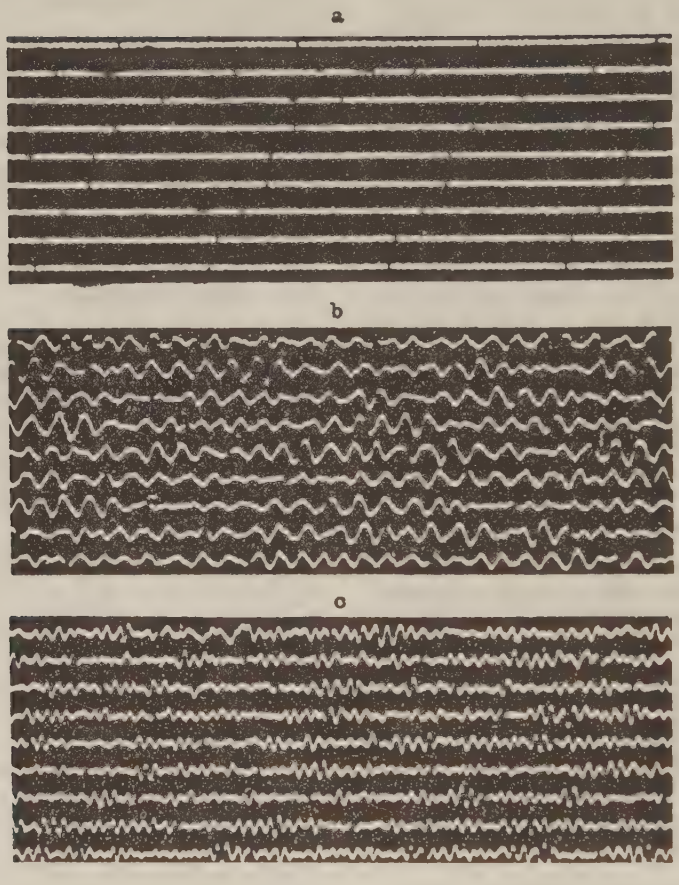

Fig. 12 Vertical seismograms, registered on the Galitzin seismograph at De Bilt, Holland.

a). Day of microseismic calm 31 July - 1 August 1953
b). Microseisms caused by a depression over the Atlantic, 22 - 23 December 1953
c). Microseisms caused by a depression over the North Sea, 8 - 9 August 1948

The relation between actual and registered amplitudes is 1 : 725 for b), and 1 : 575 for c). 1 horizontal centimetre covers 20 seconds.

wind in Lough Neagh (N. Ireland) makes for good fishing in the Bann river, which flows from the northern side of the lake. At Windermere lake (England) on the contrary, a northerly wind, blowing towards the outlet there, is regarded as having the same effect on the fishing in the lake's outflow.

Deelder (1953) tried to get a correlation between wind direction and catches in the IJsselmeer (Holland). This lake is barred from the sea by a 35 km dike, provided with a set of sluices at each end. Consequently a big fyke net fishery for silver eels has developed here. Catch results revealed that with strong westerly winds relatively many more silver eels (83½% of the total) are caught at the eastern side than in periods with moderate easterly winds (50%). One may presume that wind strength is also of importance here, as a strong wind makes itself felt more than a weak one.

Wind influence is clearly demonstrated in the Baltic too, e.g. along the Rügen-coast (Rumphorst, 1930; Meyer, 1938; Nolte, 1938) with its several bays facing different directions. Winds undoubtedly increase eel catches on those sections of the coast towards which they blow. As eels are caught here with fyke nets connected to the shore, this phenomenon consequently also demonstrates that with coastal winds the silver eels come quite near the shore. According to the same authors the wind influence is likely to be transmitted to the eels by the different wind-generated sea currents, but this certainly does not explain the eels' close approach to the shores bordering the huge Baltic.

c) Artificial light

Persistent reports from fishermen indicate that artificial light may deflect the migration route of silver eels, e.g. street lights along a riverbank may cause much reduced catches at the lit side. Petersen (1906) mentioned several of these fishermen's allegations, and Rumphorst (1930) too cites an example at Rügen in the Baltic, where catches at a certain site only increased when the bathing season was over and the lights on the nearby promenade had been extinguished. It is of importance to notice that all these cases relate to a number of faint lights placed well above the water surface. An experiment of Petersen (1906) using kerosene lamps confirmed this deduction. When using a strong light-beam in shallow clear water, Petersen moreover could clearly show a shunning of the light by the silver eels. His experiments, however, were not continued.

Lowe (1952) made several experiments in English brooks with underwater lights of 2 to 4 W and stated that the migration of silver eels may be deflected by them. In that case, however, the light-beams had to be pointed well upstream; when shining vertically downward they were less effective. In her laboratory experiments, silver eels chose a dark channel in preference to a lit one. In field experiments, on the contrary, silver eels migrating downstream did not choose the dark side more often than the lit one when a bright light was presented. A very remarkable result was moreover that artificial lights had most effect on those nights when the eels were most active.

Braütigam (1961) experimented extensively at the Rügen coast with a range of unbeamed underwater lights and concluded that on some nights catches at certain sites could be increased several times.

It is certain that silver eels may react to artificial light; how this phenomenon is evoked, however, is by no means known. Without doubt the degree and kind of turbidity of the water play an important rôle, together with the intensity and type of light-source. Due to these factors among others, the whole phenomenon is still of such a confusing nature that no reliable procedure has been found for diverting silver eels with light towards certain catch sites and so increasing the catches.

Apart from very occasional and scattered trials, no regular use of light to influence the commercial catch of silver eels is known, and this provides the best proof that this system does not yet work satisfactorily. The only exceptions known are those at Comacchio near Venice and in Irish rivers. At Comacchio, fishermen used fires to reduce the intensity of large migrations and to calm down the silver eels already caught (Walter, 1910). Irish reports tell of blazing torches placed to check the run of silver eels while the nets were emptied (Went, 1944). It must be stressed, however, that the cases mentioned here refer to barring and not to diverting the migration.

d) Electricity

With the development of modern technical facilities, people have naturally considered the possibility of influencing the migration route of silver eels with use of electricity, aiming at an increase in catches by guiding them towards previously selected catch sites. The mere fact that this technique is not universally used, is a sign that, up till now, sufficient knowledge about the subject is lacking. Of the trials made here and there, it is of interest to mention here one, carried out in the river Shannon (Ireland) on behalf of the Electricity Supply Board.

A gap with a width of about 12 m was barred by three nets, side by side. In front of the

middle net a positive electrode and, more upstream, at each bank a negative electrode was placed. Tests were made at a terminal voltage of 250 and an electrode loading of 7 amps. The gap was fished for ten consecutive 2- hour periods with the electrode alternately "on" and "off".

In the five 2-hour periods with the electricity system switched "on", the catch of both side nets amounted to 31.8 kg each and that of the middle net to 108.1 kg. The five 2-hour periods with the electricity system switched "off" resulted in total catches of 54.1, 73.1 and 117.7 kg respectively. From these results one gets the impression that: a) not all silver eels let themselves be guided towards the positive electrode but only about the half of them; b) the total catches without use of electricity are conspicuously greater.

Obviously many silver eels are repelled by an electric field and seek other possibilities to escape.

Uninfluenced migration

Real uninfluenced migration is only possible in huge water-stretches, such as the sea. As a matter of fact it is very difficult to catch migrating silver eels at sea, and if the eels tend to swim at great depths it will become technically impossible to catch them, the more because migratory fish can be caught best by stationary gear.

It has been shown possible to catch silver eels in the shallow waters along the continent, e.g. in the North Sea, with fast-moving towed nets, but from these rare catches no consistent data about the migration route or intensity of migration can be derived.

Great quantities of migrating silver eels can only be caught by stationary gear, e.g. fyke nets, standing at that part of a coast where the eels concentrate. If such a situation is used for marking experiments, distinct results may be acquired. Some of these investigations, will be discussed here.

Lüthmann and Mann (1958) marked silver eels and released them at Gorleben on the Elbe. Two of these were recaptured on the Danish North Sea coast, thus showing movement in a rather unexpected direction, which result, however, was also obtained by Tesch (1974). He liberated silvereels, tagged with ultrasonic transmitters, near Heligoland and observed at 6 of them a swimming direction of 340°, or N20°W. In the Baltic the silvereel migration shows quite a different pattern, according to the illustrative results of the marking experiments carried out by Määr (1947) during the period 1937 to 1939.

When considering Määr's results plotted on a map, one is convinced that the uninfluenced migration in the Baltic proceeds like that of birds, viz. over a broad front in a certain direction. If such a migration strikes an impassable area, in this case a coastline, the phenomenon of the concentrated migration is evoked, running in that direction along the coastline that corresponds most nearly with the original direction of migration. (cf. Deelder, 1970).

From the recaptures in Määr's experiments (Fig. 13), it is obvious that the uninfluenced migration route runs in the direction about 240° or W 30°S, so that the Baltic is definitely crossed. This explains fully the concentrations of silver eel fisheries in certain area's, e.g. at the western side of the Baltic, which are fixed by the areas of departure at the other side of the Baltic, i.e. by the big river mouths at the eastern side.

Määr's results, moreover, give rise to some more considerations. One is that the silver eels certainly are not migrating with the help of a "sense of geographical position", which sometimes is ascribed to animals by migration experts. In that case the silver eels should try to reach their spawning area by the shortest way, namely the great circle route through the start (Baltic) and finish (Sargasso Sea) of the migratory journey. They then should migrate in the direction about N 80°W (Deelder, 1949), which is not their migration course there (Deelder, 1970).

A third region where observations on the uninhibited migration of silvereels have been carried out is the Bay of Biscay. Here Tesch (1978) liberated silvereels with ultrasonic transmitters and found the mean direction during off-shelf migration to be about 260°, or W10°S.

Comparing these results: 240° in the Baltic, 340° in the German Bight and 260° in the Bay of Biscay, one has to consider the possibility that silvereels are able to fulfill the "angular migration", i.e., in different regions different courses, like some bird species as for example the Scandinavian Chaffinch, Fringilla coelebs (Tinbergen, 1967). In the Baltic the 240° course leads the silvereels toward the outlet; in the North Sea heading 340° brings them to the Atlantic (apparently the Strait of Dover is not incorporated in eel's migratory behaviour) and from SW Europe the 260° direction nearly coincides with the straight course toward the Sargasso Sea (from Cape Finisterre about 255°).

Fig. 13 Map showing the results of marking-experiments with Baltic silver eels, carried out by Määr (1947). The places of recaptures show clearly the existence of concentrated migration along certain coastlines originated by a broad-front crossing of the Baltic in a direction about N 120° W. (Encircled marks show the places of release).

When discussing the orientation of silver eels it must be remarked that Edelstam (1965) ascertained by tank experiments that silver eels possess a star-compass mechanism. He also tried to investigate the orientation of silver eels in the Baltic by tagging them with long-stringed baloons before releasing them off the southern coast of Sweden. The uniform behaviour of the animals on each occasion was striking. Immediately upon release, they would often rush into deep water in arbitrary directions and sometimes continue on those courses for a few minutes, but within a short time they would all, or nearly all, head in the same direction. On two particular days the majority of the eels had already chosen a direction before touching the water. They would twist in the hands of the operator so as to point their heads in the final vanishing direction, and then rush off in that direction immediately on release. It could be ascertained that the precision of orientation was not associated with the visibility of the sun nor with the time of day or night.

Marking experiments also offer the possibility of getting an idea about the migration speed of silver eels. Lühmann and Mann (1958) mentioned a minimal speed of 13 km a day, fitting well with values mentioned by Trybom and Schneider (1908), who also found in their experiments maximum speeds up to 50 km a day, together with average top speeds of about 36 km a day. These data have been nicely confirmed by Määr (1949) who found maximum speeds of 62.8 km and 54.5 km a day and average high speeds of 25 to 30 km a day. The average travelling rate was much less, viz. 16.4 km a day. Considering these values, one must bear in mind that these eels had been caught by fyke nets, which were only emptied during the morning, so that the eels may have stayed for several hours in the fyke nets already. As the top speed of 62.8 km a day was developed by an eel which was only 42 h under way, covering a distance of at least 110 km, the possibility is great that the actual speed was higher.

Telemetric observations of Tesch (1974; 1978) also revealed swimming speed data: maximum speeds over a period of 1 h: 4.15 km for silvereels and 6.22 km for yelloweels, while Westin and Nymann (1979) found 2.2 km/h as max. speed for silvereels in the Baltic. There are strong indications that the initial migration of silver eels takes place in the upper water layers. Petersen (1906) stated as his conviction as well as that of many Baltic fishermen "that most of the eels go over the guides of the traps". Blegvad (cf. Sch.1929), when on board of a ship equipped with a search-light, observed a distinct migration of silver eels in the upper water layers of the Great Belt. He mentioned the slow movements of the eels, with which they kept themselves up, while being transported by the fast water-flow towards the North Sea.

A possible adaptation to life at the surface is seen in the pure white belly of the silver eel contrasting sharply with the coloured belly of the bottom dwelling yellow eel. Such a white ventral side will be most effective in the top water layers, preventing the body contours from contrasting strongly with the light water surface; contrasting coloration would undoubtedly result in attacking predators coming from beneath. In that case the silver eel would be helpless.

A surface migration would tally well with the silver eel's ability to orientate itself by by using star-light (Edelstam, 1965). This will only be of biological value when swimming at the surface.

Probably the star-compass mechanism is made possible by transformation of the silver eel's eye before the seaward journey. According to Carlisle and Denton (1959) and Stramke (1972) this transformation, in which the eye becomes larger with a relatively even larger pupil, makes it a more efficient light collecting organ, whilst also the increase in the total retinal density of photo-sensitive pigment makes the retina more efficient in usefully absorbing the light incident on it.

In this respect it may be mentioned that Tesch (1978) with his telemetric observations demonstrated that silvereels are extremely sensitive to light. Vertical migration in sea takes place at dawn and dusk over a range of several hundred meters.

The silvereels' surface migration in the coastal sea, mentioned before, is the last aspect of the eels' activity which can be observed properly during its life span. From certain observations, however, one may draw deductions about what happens afterwards. Although Boëtius and Boëtius (1980) treated silvereels with hormones and got strip-ripe animals of which interesting photographs are shown, one cannot assume that these fish should be able to cover a huge stretch in the Atlantic with their belly full of swollen gonads. Hence, one has to conclude that the fish produced by the authors are not in concordance with those that cross the ocean first and then develop for the spawning act.

Svärdson (1949) described four eels caught in swedish waters in, what he calls, "partial nuptial dress". These eels undoubtedly give the impression of already possessing many of the characters which might occur during the trip through the Atlantic.

All four had enlarged eyes, with a diameter of about 1 cm; the pectorals were almost black, some of them very pointed and lengthened; moreover, the snout of the animals seemed to be more or less blunted. Finally, the ventro-lateral parts of the body were not as white as usual with silver eels but had assumed a rather reddish-brown colour.

Some years afterwards Rasmussen (1951) also mentioned the catch of two female eels, both with big eyes and black pointed pectorals (one pair bilobate) and one with bronze coloured sides. Wundsch (1953) mentioned some eels with strikingly big eyes and a bronze coloured ventral side.

As these characteristics must be considered as premature anomalies, they give some indications of the way of life which may be expected during the Atlantic journey. Undoubtedly the very large eyes point to a deep-sea life, in complete contrast to the silver eel stage to which we earlier ascribed a life in the surface water layers. This conclusion is in agreement with the much darkened underside of the body. A white belly would be of no use in the deep sea.

An excellent indication of a future deep-sea life has been discovered by Carlisle and Denton (1959), who studied the eyes of eels. They observed that the retina of silver eels change to a golden colour, like that of the photosensitive chrysopsius of deep-sea fish. The maximum of absorption shifts by about 33 mu towards the shorter wavelength end of the spectrum, and the final total retinal density curve of the silver eel is almost identical with that of the conger eel, Conger conger (L.), and of a deep-sea eel, Synaphobranchus sp. Their conclusions have been confirmed by Stramke (1972) and Pankhurst and Lythgoe (1983).

The peculiar change in the pectorals offers us a tentative explanation for the eel's way of life in the deep sea too. Strong elongated and pointed pectorals indicate a behaviour that results in swimming long stretches at constant depth, which only now and then is changed and then kept constant again. Tunnies and horse mackerels are good examples of this way of life.

Round pectorals, on the contrary, indicate a swimming behaviour in which the level is continually changing, so that the fish is well adapted to overcome obstacles and find its way through them. Groupers, tenches and silver eels are good examples of this.

The phenomenon that after the silver eel stage the eel acquires elongated pointed pectorals is in our opinion a strong indication that it changes over to swimming for long uninterrupted stretches at a certain level.

With regard to a discussion whether eel is able to cross the Atlantic or not to reach its spawning area (cf. Tucker, 1959; d'Ancona, 1959a, 1960; Jones, 1959; Deelder, 1960a; Gemeroy and Boyden, 1961; Sinha and Jones, 1976b) the attention might be drawn to the study of Boëtius and Boëtius (1980) who concluded that the total energy reserves of a silvereel are sufficient to cover the costs of a 4 000-km active migration and full sexual development as well.

3.52 Schooling

The eel, in all its stages, is an individualist. Virtually no schooling, where the individuals react towards each other, can therefore be noticed. The "schools" of elvers and young eels which are observed from time to time in estuaries and rivers are the result of a mass response to outward conditions and not of active assembling.

A certain phenomenon might be regarded as a kind of schooling, namely the massive "balls" of silver eels which sometimes allegedly come downstream in a river, but this can be explained by their urge to keep in close contact with an object, starting with some debris and ending with silver eels themselves. (cf. Nilsson, 1860). This phenomenon, however, seems to be extremely rare and no comprehensive data are available.

3.53 Responses to stimuli

Environmental stimuli: Influence of mechanical stimuli, as e.g. vibrations, may be observed during migration; see 3.51. With regard to chemical stimuli it has already been pointed out that eels are highly sensitive to olfactory impulses. Teichmann (1957) showed that eels are able to perceive B-phenyl-ethyl-alcohol in a concentration of one part in 2.857×10^{18}. He concluded that a monomolecular stimulation is highly likely. In this respect the attention must be drawn to: a) the impressive bulbi olfactorii of the eel (Lissner, 1923), which demonstrate the great importance of olfactory stimuli; b) the entrance of the big nose-cavity, which is tube-like and starts immediately over the mouth (see also 3.41).

Muir Evans (1937) studied the brain of the eel and observed a remarkable resemblance to the brain of the common sole (Solea solea): a highly developed olfactory system together with well-marked facial and somatic sensory lobes and small optic lobes, which features are related by him to the eel's feeding habit by smell, taste and touch during the night.

This view apparently is justified, as Pankhurst and Lythgoe (1983) found the olfactory organs to atrophy in matured eels, thus with feeding stopped.

For the influence of temperature upon migration, see 3.51. Boëtius and Boëtius (1967), in their profound study, mentioned the influence of water temperature upon respiratory rate and heart rate, with a maximum at 25 to 26°C. Investigations of Deelder (unpublished) showed that eels become highly active at a water temperature of about 20°C and higher.

Optical stimuli: see 3.51. As has been mentioned before, eels shun daylight, although some activity may take place then.

Artificial stimuli: Highly repellent are such artificial stimuli as objects drawn over the bottom of the water, as is the case with eel trawls. Regular eel trawling, which e.g. occurred at the IJsselmeer up till 1970, obviously causes a spreading terror among the eel stock, resulting in diminishing catches, of e.g. fyke nets situated near the banks.

4 POPULATION

4.1 Structure

4.11 Sex ratio. See under 3.11

Sex composition may vary exceedingly, from nearly 100 per cent males in river estuaries to 100 per cent females in tributaries of big rivers and in coastal waters. Compare, e.g., Penáz and Tesch (1970): the percentage of females is highest in the vicinity of Heligoland. It falls to the lowest value in the inner estuary of the Elbe and rises again above Hamburg to the high value typical for most inland waters.

4.12 Age composition

Because of frequent neglect of the existence of supernumerary zones in eel otoliths (cf. Deelder, 1981), reliable eel age data are few. It may be presumed that no correlation exists between age composition and such items as depth, time of day, season, etc. Density of age-groups is mainly determined by the size of elver immigration or by stocking rates. See 3.31 and 3.43.

4.13 Size composition.

In enclosed areas, size composition is dependent on immigration and stocking. In unenclosed areas, in view of the eel's habit of migrating regularly, no consistent composition occurs. See 3.43 and 3.513.

4.2 Abundance and density

Calculations about the density of eel stocks, the eel being an elusive fish, are almost impossible. According to Havinga (1945), one eel per 9 m^2 lived in the IJsselmeer, but density in river-mouths may be far higher and in tributaries far lower. Muus (1967) found in Danish fjords, at places with a dense vegetation of Zostera, a density of 0.5 to 5 eels per 10 m^2 and in wintertime he noticed once a density of 4 eels per m^2.

Under artificial conditions very high densities may be attained: Meyer-Waarden and Koops (1968) got an excellent growth of pond-eels with a density of 1.8 eel per m^2. For the Comacchio lakes about 1975 Rossi (1979) calculated 265 eels/ha, producing a catch of 61 silvereels/ha.

4.3 Natality and recruitment

No reliable data are known.

4.4 Mortality and morbidity

Mostly because of the secret life and the different environmental conditions occurring in the eel's area no reliable data are available. Factors affecting mortality are discussed under 3.2, 3.34, 3.35 and 5.4. Concerning the physical factors affecting mortality, mention must be made of elvers and eels migrating towards inaccessible or uninhabitable areas and of winter mortality due to freezing of the water followed by lack of oxygen (Muus, 1967).

4.5 Dynamics of population

Deelder and de Veen (1958) tried, with regard to the eel fisheries of the IJsselmeer, to calculate the consequence of a possible raising of the legal minimum size. For this purpose they built a 3-dimensional model using the following simplified formula, which is based on the ideas of Beverton and Holt (1957):

$$Vw = \frac{FR\, e^{-M(t_{\varrho}^{1}-t_{\varrho})}}{F+M}\left[1-e^{-(F+M)}\right]\sum_{q=0}^{t_{\lambda}-t_{\varrho}^{1}-r} e^{-(F+M)q}\, W_{t(\varrho^{1}+q+r)-(\varrho^{1}+q)}$$

Vw : weight of total annual catch
F and M: coefficients of fishing and natural mortality
t_{ϱ} : moment of entering the IJsselmeer as elvers
t_{ϱ}^{1} : moment of entering fishery
t_{λ} : moment of leaving the IJsselmeer as silver eels
R : average magnitude of elver stock entering the IJsselmeer
Wt : weight of eel at the moment t.

4.6 The population in the community and the ecosystem

This subject is sufficiently dealt with in the preceding part of the synopsis.

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gears

Study of the extensive reports on this subject by Meyer-Waarden (1965, 1966, 1967) and McGrath (1971) are strongly recommended.

Elvers may be caught either in an active or in a passive way, adapted to their behaviour. In the active fishery scoop-nets are used together with a faint light to attract and concentrate the elvers, e.g., in rivers which are invaded by masses of elvers as is the case in southern and mid-European countries and England (Severn). Also nets drawn by boats are used in open water stretches, as in the Atlantic off the French coast. Sometimes a seine net is pulled through an area with elver concentration, e.g., in Dutch shiplocks, cf. for France: Elie (1979), Cantrelle (1981); for England: Fischer and Lübbert (1911), Deelder (1955).

In the passive way, migrating elvers are induced by a small artificial tricklet of fresh water, flowing along a gentle slope, to break the surface and mount the slope until at the end of it they tumble down into a basin (O'Leary, 1982).

Eels are caught in many ways, adapted to the peculiar behaviour of the fish in connection with local circumstances. Here too, catching methods may be classified into an active and a passive category.

The most important active fishing gear is the eel trawl, which is forbidden in most freshwater areas because of its destructive action upon fish stocks. A notorious example of a freshwater eel trawl was that of the IJsselmeer (Holland), a remnant of the former Zuyder Zee. Willfull sea trawling for eels occurs e.g. in Heligoland Bight. Sometimes in coastal waters trawls designed for other purpose, e.g. shrimp trawls, are used to catch eels.

Another active catching method is that with use of eel spears (Went, 1952; Wundsch, 1962) and eel combs, either manipulated when walking or from a vessel. Anglers may catch eels with baited hook or by "bobbing", i.e. with a mass of strung worms, which may be surrounded by a piece of nylon stocking. Advantage is taken of the tenacity of the eels, to hoist them above water over a container into which they are dropped. Sometimes dip-nets are also used.

A system which has come into use in recent times is fishing with an electrified scoop net. Fishermen may try in this way to reach inaccessible or unfishable places, e.g. stony or weeded banks of canals, and catch eels here which otherwise would have escaped.

Catching methods with long periods of fishermen's inactivity are also numerous: e.g. fyke nets, eel-pots, baited hooks. With the well-known fyke nets the fishermen make use of the eel's tendency to swim along walls. A leader of netting guides the eels into the trap-net provided with funnel-shaped inlets which block the eels' return to freedom. Fyke nets are considerably adapted to local circumstances: small ones may be used in the smallest ditches, really huge fyke nets are used in open sea (cf. also Meyer-Waarden, 1965, and '65, '66, '67; Loebell, 1965).

Eel-pots may be considered as small fyke nets with a rigid frame, without a guiding system. The attracting agent is formed by the bait put into the pots, or by the darkness when the pots are tube-like with solid walls. A useful combination of these demands is formed by the wooden tube-like baited eel-pots with two entrances, which recently have been put in use in Holland with considerable success.

Baited hooks are commonly used and may be attached to floats separately or with a short sideline to a common long line which may attain a length of several kilometres.

Silver eels. Because of their restlessness, stationary gear is generally used to catch silver eels. In flowing rivers the great difficulty is to sift the eels out of the water without being hampered too much by the floating debris, so common in autumn, and without barring the flow too much, as this will result in deterring the silver eels, or, near powerplants, will influence the output of them in a negative way. Very long funnel-shaped nets, which possess a high water permeability, are the only answer to this problem. These nets may be fixed in a rigid frame, either connected to the banks or to a weir, so that the whole flow may be forced to pass through the net, or operated from an anchored ship as occurred so often at the river Rhine (Bürger, 1926). An adapted type is the so-called "Scherbrett-hamen" in use on some German rivers. This net, among the largest freshwater-gear in the world, has the mouth kept open by a trawl-type plate put obliquely in the waterflow. (Meyer-Waarden, 1965).

When the waterflow is small, e.g. in brooks, an efficient fishery may be carried out by forcing the water over a lot of horizontal gratings, where the water falls through and silver eels, together with other fish and objects, stay behind.

In great open-water areas silver eels are mainly fished with giant fyke nets, as e.g. along the coasts of the Western-Baltic. Small areas with a narrow outlet without a heavy flow are fished in a easy way: barring the outlet with diverging walls protruding into a catchroom. These walls of course may be built of any suitable material available. Well-known examples of this type are the catching-sites at Comacchio (Lübbert, 1908).

Again another catch-method in a small canal is to bar it with netting during the evening and night (to be lowered for passing ships) and catch the searching silvereels with fykenets, set out near the barring net.

Along the North-Sea coasts silver eel fishing in the autumn has been carried out in recent times by pairs of trawlers, towing one net between them, in this way obviously getting the necessary speed.

Because of the great diversity in local circumstances under which eels and silver eels are caught, it is virtually impossible to describe exactly all compositions and components of which the gears exist. All material available and suitable may be used and is used, not only e.g. hemp, silk, cotton and nylon, but also e.g. concrete, wood, iron, reeds, etc.

Except for the use of a faint candle or kerosene light with scoop-net fishing for elvers no practical use is made of light, nor of other agents such as echosounding, sound, etc., when fishing for this species.

5.12 Boats

The already mentioned diversity in circumstances under which eels and silver eels are caught, exerts its influence on the boats too. These may range in size from one-person paddle-canoes, as in use e.g. in the Neretva-delta (Yugo-Slavia), to the heavy trawlers, able to withstand stormy weather at sea.

5.2 Fishing areas

In many areas fishing occurs the whole year round; in colder areas it is interrupted by hibernation of the eel (see also 5.43).

Peaks of fishing for eels occur when the water temperature has reached summer-values. Fishing for silver eels and elvers only takes place during the migration (see 3.51).

5.4 Fishing operations and results

5.41 Effort and intensity

Because of the numerous catch-methods under very different circumstances no uniform data can be given about the aspects of effort and intensity of the eel fishing, the more as data produced by fishermen with fair certainty are fully unreliable (see also 5.43).

With the former trawl fishing on the IJsselmeër a higher fishing intensity obviously resulted in a lower yield (Deelder, 1965; 1970).

5.42 Selectivity

The catch-size of the round and slippery eel is very dependent on the mesh-size of the gear. Comparative investigations on this subject have been carried out simultaneously in the IJsselmeer (Deelder, unpublished) with eel trawls of different mesh-size, viz. 14, 17 and 22 mm, when stretched. The results of these trials are shown graphically in Fig. 14.

Of course hook size, when baited hooks are used for eel fishing, exerts a selective influence too. So does the size of the bait, the length of the connecting lines and the size-composition of the eel stock. As a matter of fact the latter item also affects catches with nets, clearly demonstrated when catches of fyke nets with same mesh-size and operated in two separated water-areas were compared (Fig. 15, Deelder, 1968).

5.43 Catches

Because of the secretiveness of eel fishermen it is almost impossible to get reliable catch data; hence, one must conclude that statistics (cf. Table VII) are highly untrustworthy. A good example of this aspect was recently obtained from the IJsselmeer fishermen in Holland. Officially about 800-900 t are caught annually in this lake (180 000 ha). When, however, the Government considered reclamation of a certain area, the fishermen started in 1983 a protest and all of a sudden mentioned a total catch about 2½ times higher. Considering their standard of living, this amount certainly was not exagerated.

For the sake of completeness, some data about catches are referred to here. Meyer Waarden (1965a; 1966; 1967) in his compilation on the eel fisheries in West Germany presented catches in several parts of the country. In total for inland waters about 1 000 t/year. Saint Paul (1977) estimated the catch of small eels in the German Bight about 90 t/year. Later on Aker and Koops (1979) discussed catches in the same area: 220-270 t/year, of which by trawling nearly 100 t/year. According to Moriarty (1981) the catch of the Irish Republic amounts to 150 t/year. Rasmussen and Therkildsen (1979) calculated for a Danish brook a production of 9.3 g/m^2/year. Rossi (1979) mentioned for lakes near Comacchio (Podelta) a catch of 19 kg/ha/year, comprising 61 animals. Finally Leopold and Bnińska (1982) discussed an annual catch in Poland of 2 477 t, of which 1 789 t recreational. A special catch aspect is created by elver fishing in the areas with accumulation during the inward migration, e.g., Churchward and Hunt (1977) mention an annual catch of about 100 t in the Severn Basin, whereas Cantrelle (1981) and Elie (1979) discussed French elver catches, resp. at the Gironde (400-800 t/year) and Loire (much more than 1 455 t/year).

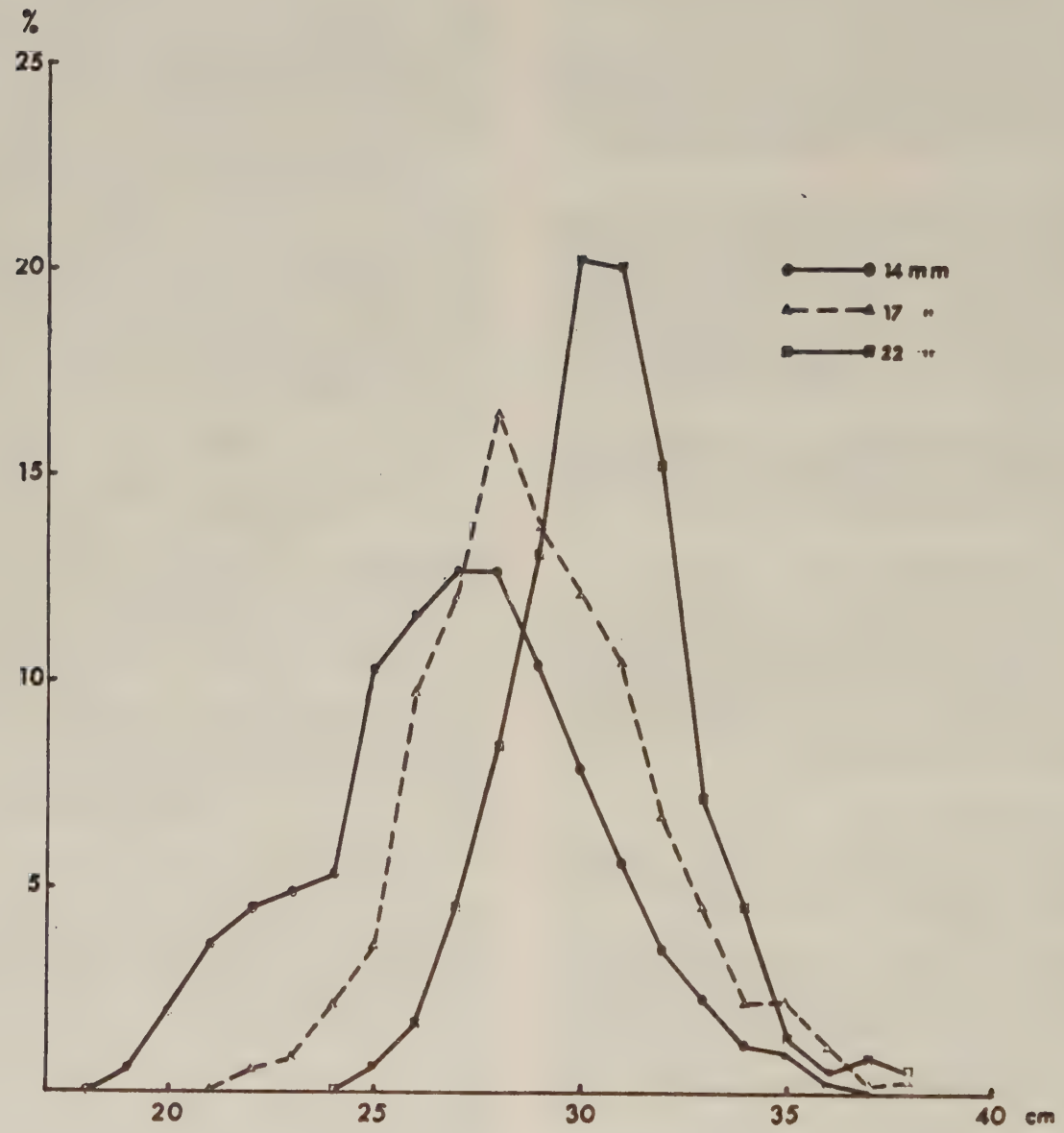

Fig. 14 Length-frequencies of IJsselmeer eels, caught by eel-trawls with different mesh-sizes in the cod-end, viz. 14, 17 and 22 mm respectively when stretched.
Eel-lengths rounded off to the nearest cm downwards.

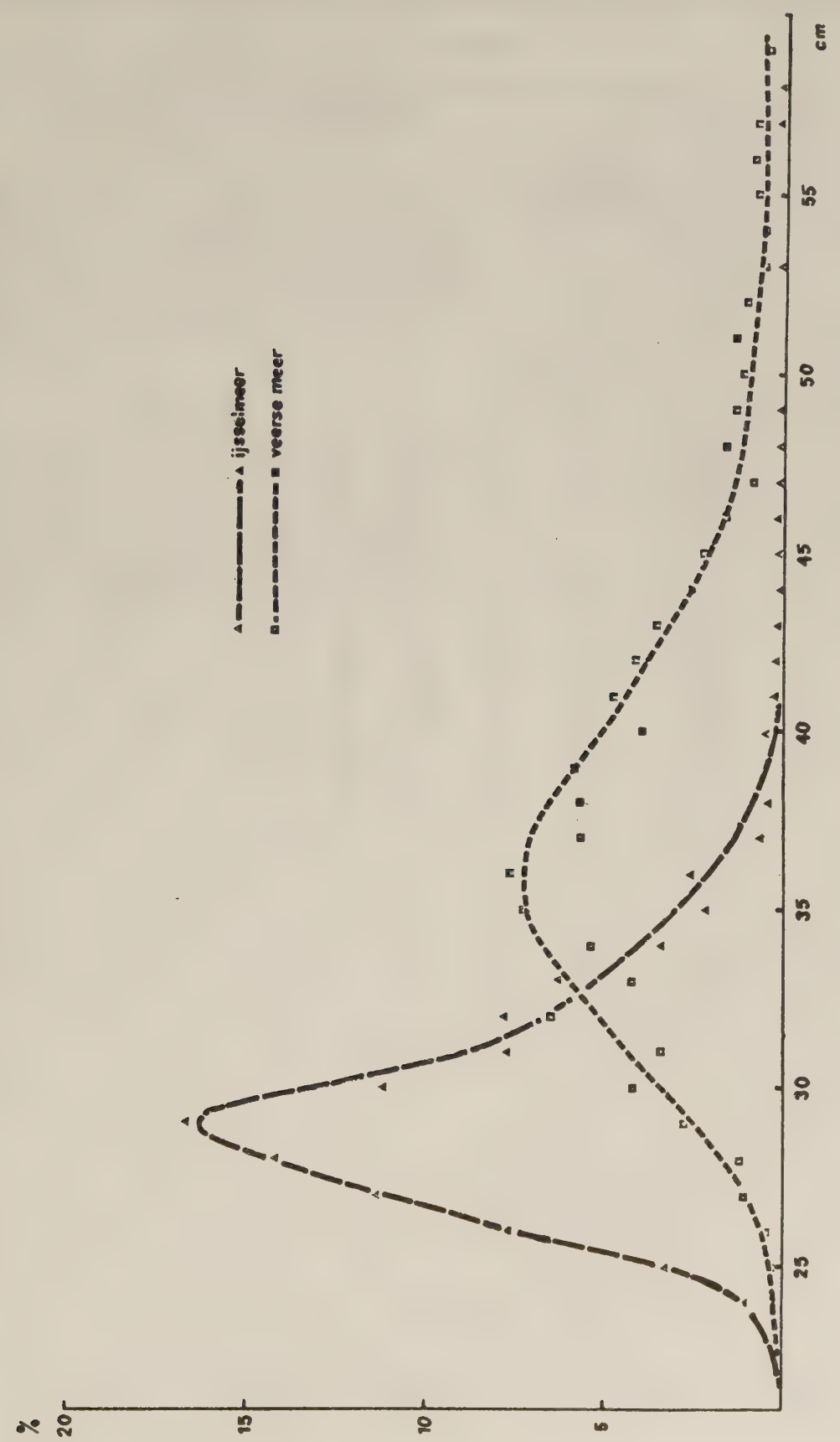

Fig. 15 Length-frequencies of eels caught by fyke-nets with same mesh-size (viz. 18 mm when stretched), in IJsselmeer and Veerse Meer. Eel-lengths rounded off to nearest cm downwards.

TABLE VII

Eel catches (FAO Yearbook of Fishery Statistics 1981, Vol. 52)

SPECIES / ESPECE / ESPECIE	FISHING AREA / ZONE DE PECHE / AREA DE PESCA	1978 MT	1979 MT	1980 MT	1981 MT
EUROPEAN EEL ANGUILLE D'EUROPE ANGUILA EUROPEA		ANGUILLA ANGUILLA 1,43(02)002,01 ELE			
ALGERIA	01	0	0	0	0
MOROCCO	01	0	0	0	0
AREA TOTAL	01	0	0	0	0
TURKEY	04	283	396	224	374
AREA TOTAL	04	283	396	224	374
DENMARK	05	44	34	113	141F
FINLAND	05	62	61	63	32
FRANCE	05	...	...	2582	...
GERMAN DM RP	05	634	608	595	595
ITALY	05	555	665	543	530
NETHERLANDS	05	748	552	690	723
POLAND	05	670	713	504	703
SPAIN	05	600	300	300	400
SWEDEN	05	...	...	...	-
AREA TOTAL	05	3313	2933	5390	3124F
USSR	07	1348	543	1079	176
AREA TOTAL	07	1348	543	1079	176
DENMARK	27	2335	1826	2141	2121F
FINLAND	27	15	16	16	8
FRANCE	27	65	1083	909	335
GERMAN DM RP	27	209	208	126	114
GERMANY FR	27	319	348	330	316
IRELAND	27	76	110	75	94
NETHERLANDS	27	143	177	187	175
NORWAY	27	347	374	387	369
POLAND	27	271	294	406	49
PORTUGAL	27	44	25	32	33
SPAIN	27	...	66	44	148
SWEDEN	27	1076	956	1112	887
USSR	27	170	89	161	139
UK ENGLD WAL	27	19	29	53	69
UK NO IRELD	27	858	850	1000	789
AREA TOTAL	27	5947	6451	6979	5646F
MOROCCO	34	2	2	5	26
SPAIN	34	-	-	-	-
AREA TOTAL	34	2	2	5	26
FRANCE	37	1875	2061	1012	1591
ITALY	37	1682	1757	1721	1758
MOROCCO	37	-	19	0	0
SPAIN	37	55	94	-	-
TUNISIA	37	90	93	423	441
YUGOSLAVIA	37	56	38	44	35
AREA TOTAL	37	3758	4062	3200	3825
ITEM TOTAL	S	14651	14387	16877	13171F

Codes: 01 African inland waters
04 Asian inland waters
05 European inland waters
07 Soviet inland waters
27 NE Atlantic area
34 E Atlantic area
37 Mediterranean and Black Sea

N.B. According to these data, there should be for example no eel catch in West German inland waters, and no recreational catch in Poland (cf. 5.43)

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.11 Limitation or reduction of total catch

No instances are known of limitations on the efficiency of fishing units or on total catches (quota). Limitation on the number of fishing units (fishermen), which may be observed here and there in inland water-areas is more resulting from the urge to ensure a reasonable living than from the desire to protect the eel population.

6.12 Protection of portions of populations

The protection of portions of eel populations is enforced in only a few areas, with the idea of sheltering very small eels lest the incomes of the eel fishermen be endangered. The protection may be based upon enforcing a minimum length or minimum weight. Some instances may be mentioned here: Holland, 28 cm; N.Ireland, 5 oz (= 141.6 gr); Poland, 125 gr.

6.5 Artificial stocking

It is not possible to track all the stocking-programs carried out with eels and elvers, which are of national, international and even intercontinental nature. E.g. in 1969, 50 t of elvers were transported from France to Japan, which country also regularly receives elvers from the Severn (Churchward and Hunt, 1977).

Two instances important of elver stocking in European waters might be mentioned here. Leopold and Bnińska (1982) discussed stocking of the Polish inland waters and concluded that this lead to a real yield of 4.6 kg/ha, whereas 11.7 elvers are needed to obtain 1 kg (=2 eels).

According to Jagsch (1982) the Neusiedler See has been stocked annually since 1958; since 1975 with 4 million elvers each year, resulting into a catch of about 210 t/year (7 kg/ha). This means that about 17 elvers are needed to produce 2½ eels, weighing 1 kg together.

7 EEL CULTURE

General Remarks

Considering the results obtained by eel culture farms in southern Europe, especially in Italy, which are in operation on a solid economic base for several years, one must conclude that problems going with eel culture have been mainly, or even fully, solved there. This in sharp contrast to the opinion of eel culturists in the northern part of Europe, which needs explanation. It might be brought about that most of the northern eel culture plants operate on a small scale, diminishing the chance to develop into a viable commercial unit. For example, Anon. (1984) mentioned the setup of a Danish eelfarm, designed to produce 45 t/year, and Wickins (1983) explained that in 1982 Britain's five main eel producers together marketed nearly 100 t. Gehrke and Pelka (1982) in a study for northern European eel farms with expected annual productions of 20 t, calculated a return of at most 4%, provided the average eel weight is 230-240 g, i.e., all eels should be females, which is hard to accept.

Comparing the figures mentioned above with the annual output of Italian eel farms of hundreds of tons each, the largest producing annually about 800 t for a long period, the conclusion must be that there is indeed a huge difference in initial setup between the two European regions. A serious drawback for northern eel culturists is formed by the need to apply filters for recycled water that has to be heated; the whole system of course to be situated in expensive specially designed buildings, whereas the Italian farmer even can use open air ponds (in the Italian winter pond eels do not stop feeding for a long time if any), anyhow may refrain from heating. Besides, considering the vastness of the Italian eel farms, the presence of slow-growing eels might be accepted more easily there than in the compact northern eel farms, thus reducing culling losses considerably.

7.1 Procurement of stocks

As a consequence of eel's biology, eel culture is forced to start with either glass eels (e.g., from S. France or the Severn area, cf. 5.43) or young eels. Great quantities of these are acquired from the French Mediterranean region, while also from, e.g., the Dutch IJsselmeer and Danish waters young eels are reported to be caught for eel culture purposes.

7.2 Genetic selection of stocks

No genetic selection can be practised because of eel's biology.

7.3 Spawning

No (artificial) spawning is hitherto practised in eel culture.

7.4 Holding of stock

Either in open-air ponds or in basins under roof. In southern Europe both types are known; in the cooler northern Europe regions indoor culture with water recycling is preferred because of energy cost reasons.

7.5 Management

Successful eel culturists are not inclined to provide data on this subject, which is considered by them to be top-secret. Apparently special culture policy with remarkable results might be applied, as is demonstrated by Fig. 16, showing extraordinary lengths (average: 44 cm, SD: 3.14) and weights (average: 176.6 g, SD: 38.8) of male silvereels cultured in Italy.

7.6 Foods and feeding

See 7.5

7.7 Disease and parasite control

See Koops and Kuhlmann (1983). Quarantine of newly arrived young animals is known to be practised on eel farms.

7.8 Harvest

With all means suitable for the purpose; even suction is known to be applied.

7.9 Transport

Transport of live cultured eels is carried out in the normal way applied for eels: e.g., with motor lorries supplied with aerated tanks.

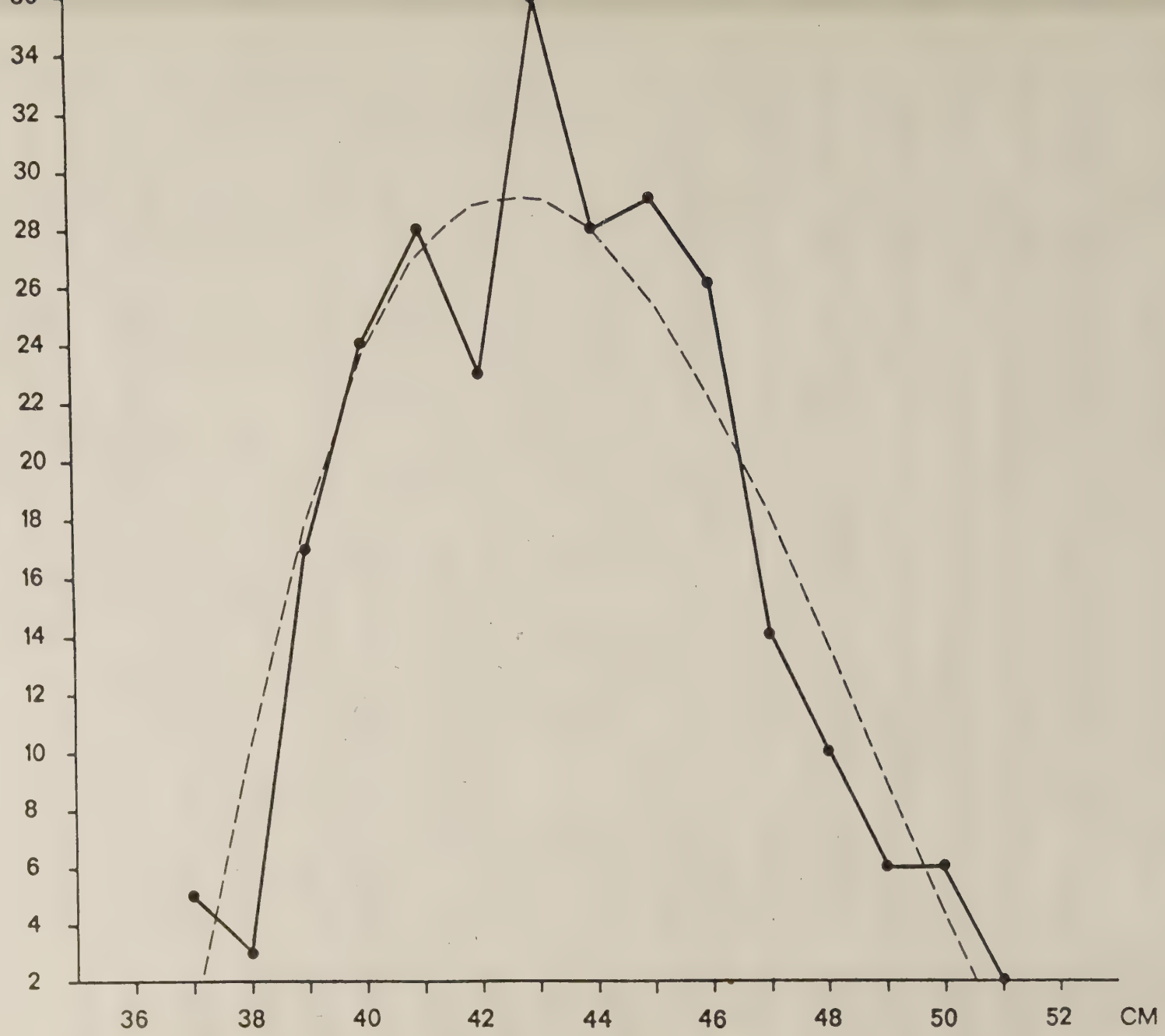

Fig. 16. Length frequency of 297 Italian cultured male silver eels. Interrupted line represents the polynomial regression: $y + Bo + B_1x + B_2x^2 + \ldots + B_nx^n$.(x = length; y = N). R = 0.93

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ISBN 92-5-102166-X